Community assembly of island mammal metacommunities: The role of the regional species pool

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ABSTRACT

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One of community ecology's fundamental challenges is to identify the community assembly mechanisms that shape diversity patterns. Previous studies have largely focused on the relative influence of neutral and niche-based mechanisms on community composition within a single region. However, the influence of the species pool on these mechanisms remains relatively unexplored, despite its potentially pivotal role in community assembly. The functional diversity available within the species pool is particularly relevant, as it could regulate how strongly species are sorted into local environmental niches. Here, we investigate how the species pool's functional diversity influences the relative importance of dispersal and environmental filtering (i.e. species sorting) in structuring taxonomic, functional, and phylogenetic β-diversity patterns within 9 insular non-volant mammal metacommunities, distributed across the globe. We find that dispersal limitation largely drives phylogenetic turnover patterns, suggesting that colonization is the primary obstacle during community assembly of insular metacommunities. However, we did not find a universal trend in the relative importance of dispersal and environmental filtering across metacommunities. The functional diversity available within the species pool was also not consistently related to the strength of species sorting. We conclude that the ecological model of species sorting does not adequately represent community assembly. This raises questions about how the incorporation of evolutionary processes such as speciation and adaptation into the metacommunity framework would improve our understanding of community assembly.

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TABLE OF CONTENTS

LIST OF TABLES AND FIGURES

In-text Tables and Figures

Appendix

INTRODUCTION

Understanding how communities are assembled can provide valuable insight into the creation and maintenance of biodiversity (Keddy 1992; Kraft *et al.* 2007). However, one of the greatest challenges in community ecology is to disentangle the neutral and niche-based processes involved in community assembly (Keddy 1992; Chase & Myers 2011). Community assembly is defined as the process where species disperse from a species pool (i.e. all species that are potentially able to colonize a focal community) to a locality, are then filtered into local niches by local abiotic and biotic conditions, and ultimately coexist within a local community (Mittelbach & Schemske 2015). Local communities can therefore be viewed as a subset of the species pool that underwent neutral dispersal at the regional scale, and were successfully filtered by niche-based abiotic and biotic processes at the local scale.

Metacommunity theory provides a conceptual framework to relate these local and regional processes with community structure, which can be used to investigate community assembly (Leibold *et al.* 2004). A metacommunity is a set of local communities that are potentially linked together by dispersal (Cornell 1985; Hanski & Gilpin 1991; Wilson 1992; Leibold *et al.* 2004). Metacommunities can also be viewed as a species pool, where all species within the network can potentially disperse to any other local community. Regional processes operating on the metacommunity therefore influence and interact with community assembly processes at the local scale, and vice-versa (Ricklefs 1987; Cornell & Harrison 2014; Mittelbach & Schemske 2015).

Metacommunity theory proposes four conceptual models of community assembly, which differ in the relative importance attributed to neutral processes like dispersal, and niche-based processes like environmental filtering and biotic interactions, in shaping community composition and structure (Leibold *et al.* 2004; Holyoak *et al.* 2005a). The neutral perspective assumes all species in the metacommunity are identical in competitive ability, dispersal capacity, and fitness, and that all patches are identical in environment conditions (Hubbell 2001; Leibold *et al.* 2004). Under this paradigm, community structure does not respond to environmental gradients and is instead predominantly shaped by demographic fluctuations and dispersal dynamics, which result in random walk probabilities of species losses and gains (Leibold *et al.* 2004). The patch-dynamic perspective similarly assumes all patches are environmentally homogeneous, but

considers species to differ in their ability to colonize, establish, and interact successfully in local communities (Leibold *et al.* 2004; Holyoak *et al.* 2005a). Species are therefore added to communities according to a colonization-competition tradeoff, where dispersal can counteract interspecific competition (Leibold *et al.* 2004). Under the patch-dynamic perspective, community structure is expected to respond to dispersal dynamics and biotic interactions, and should not vary along environmental gradients (Leibold *et al.* 2004; Logue *et al.* 2011). The mass-effects perspective similarly emphasizes dispersal's role in community assembly, but assumes environmental heterogeneity between habitat patches (Leibold *et al.* 2004). According to this perspective, strong connections between communities allow dispersal from source communities to maintain population densities in sink communities, even when species are unable to successfully establish in local niches (Leibold *et al.* 2004). Community structure is therefore regulated by source-sink dynamics that override environmental filtering, and is thus expected to differ along spatial gradients (Logue *et al.* 2011). The species sorting perspective, which will be tested in this study, emphasizes the influence of environmental filtering in community assembly (Leibold *et al.* 2004; Holyoak *et al.* 2005a). Under species sorting, species undergo stochastic dispersal to reach a local community and are then filtered into communities from the species pool based on their functional traits, which dictate their ability to occupy niches within the local environment (Leibold *et al.* 2004; Holyoak *et al.* 2005b; Logue *et al.* 2011; Mittelbach & Schemske 2015). As such, the matching of species' functional traits to available local environmental niches primarily determines colonization success, while dispersal limitation plays a secondary role in structuring communities (Leibold *et al.* 2004). If species sorting is driving community assembly, community structure should respond most strongly to environmental gradients (Leibold *et al.* 2004; Pavoine & Bonsall 2011).

β-diversity, i.e. site-to-site variation in species composition (Whittaker 1960), is a key tool to identify the neutral and niche-based mechanisms shaping community structure (Legendre *et al.* 2005). Although taxonomic β-diversity has been widely studied, simply focusing on species identities makes it difficult to identify evolutionary and ecological drivers of community assembly (Pavoine & Bonsall 2011; Safi *et al.* 2011; Siefert *et al.* 2013). Considering taxonomic, functional, and phylogenetic β-diversity patterns along spatial and environmental gradients can help to better disentangle the relative influence of dispersal limitation and environmental filtering

on ecological and evolutionary patterns of community structure (Emerson & Gillespie 2008; Graham & Fine 2008; Urban *et al.* 2008; Pavoine & Bonsall 2011).

While community ecology has recognized the interplay between local and regional processes for several decades (Ricklefs 1987), empirical work on metacommunities has generally been restricted to smaller scales and to a single region (Logue *et al.* 2011). Without comparing β-diversity patterns across multiple ecological, biogeographic, and historical contexts, it is difficult to identify generalities, and to explicitly determine the role of regional processes in community assembly. In particular, the importance of the functional diversity available within the species pool is poorly understood. The species pool's functional composition determines the availability of species with suitable functional traits for local niches, and thus likely influences the strength of species sorting processes in local communities (Zobel 1997; Questad & Foster 2008). Though few studies have empirically addressed this question, Questad and Foster (2008) found that species sorting operated more strongly when species were drawn from a more functionally diverse species pool, based on seed addition experiments in a small-scale grassland community. However, it is unclear whether these findings can be extended to broader-scale systems, as biogeographical, ecological, and evolutionary processes operate in complex ways on the species pool and the local community over space and time (Wiens & Donoghue 2004; Emerson & Gillespie 2008). The functional diversity available within the regional pool therefore likely plays a major role in influencing the strength of niche-based processes shaping taxonomic, functional, and phylogenetic community structure (Questad & Foster 2008; Pavoine & Bonsall 2011).

Island systems are uniquely convenient for addressing questions about species sorting, as they provide a rare empirical approximation of a metacommunity: island communities have clear boundaries and species can potentially disperse to any community throughout the island network (Leibold *et al.* 2004; Mittelbach & Schemske 2015). Due to their isolation and their typically low colonization rates, island habitats also offer more opportunities for species to adapt, diversify, and coexist, relative to more saturated mainland habitats (MacArthur & Wilson 1963; Emerson & Gillespie 2008; Warren *et al.* 2015). Functional and phylogenetic community structure therefore tend to be tightly linked to local niche space, due to trait-dependent colonization success and high levels of *in-situ* diversification (Losos *et al.* 1997; Emerson & Gillespie 2008; Losos & Ricklefs 2009; Jacquet *et al.* 2016). However, community assembly operates differently on oceanic islands (i.e. emerging as a result of volcanic activity or sea level decreases), where islands are

initially devoid of life, compared to land-bridge islands (i.e. emerging from a separation from another landmass through seismic activity or sea level rises), which retain part of a previous landmass' biota at the time of their formation (Warren *et al.* 2015). In oceanic island systems, colonization from the species pool is only possible through overwater dispersal, which is a strong dispersal barrier for many taxa, including mammals (Heaney 1984; Warren *et al.* 2015). Otherwise, niches are filled through *in situ* evolution (Warren *et al.* 2015). Community structure is therefore likely more sensitive to spatial gradients in oceanic island systems, where isolation regulates both colonization and *in situ* speciation, which are entirely responsible for filling local niches, compared to land-bridge island systems in which communities inherit species from a larger landmass (Warren *et al.* 2015). While both types of systems can be viewed as metacommunities, oceanic island systems approximate the species sorting model better than land-bridge island systems, as all resident species have dispersed from the species pool and successfully established within local niches according to their functional traits (Leibold *et al.* 2004). However, the possibility of describing the ecological and evolutionary properties of distinct communities, as well as the area, isolation, and climatic attributes of island habitats, makes island systems ideal for investigating the roles of neutral and niche-based processes within a metacommunity framework.

In this study, we use taxonomic, functional, and phylogenetic β-diversity patterns in 9 insular mammal metacommunities in several geographic regions distributed across the globe (Fig. 1) to investigate the role of species pool functional diversity in regulating the relative importance of dispersal limitation and environmental filtering during community assembly. More specifically, we test the hypotheses that (1) environmental filtering influences community structure more strongly than dispersal limitation, (2) species sorting universally shapes β-diversity patterns across geographic regions, and (3) geographic variation in the strength of species sorting is related to variation in the functional diversity of the species pools. We predict that (1) β-diversity will respond to both environmental and spatial gradients, but will vary more strongly along environmental gradients; (2) that β-diversity patterns will universally respond in this way to environmental and spatial gradients within all 9 metacommunities; but (3) that β-diversity patterns will respond most strongly to environmental gradients in metacommunities that recruit species from more functionally diverse regional species pools. These predictions vary slightly between primarily oceanic or land-bridge island systems, where dispersal limitation is

expected to play a relatively larger role in structuring communities in oceanic systems than in land-bridge systems. However, if species sorting is occurring, β-diversity patterns will respond most strongly to environmental gradients in both types of systems, especially in the presence of a functionally diverse regional species pool. We thus provide an unprecedented broad-scale look at how community assembly processes differ across multiple metacommunities to directly address the role of species pool functional diversity during community assembly.

MATERIALS & METHODS

Island mammal metacommunities

To determine whether species sorting mechanisms universally shape taxonomic, functional, and phylogenetic β-diversity patterns, we compared 9 insular mammal metacommunities distributed across the globe, including the Alexander Archipelago (51 islands), the Gulf of California (18 islands), the Mediterranean Sea (35 islands), the Adriatic Sea (14 islands), Japan (6 islands), Indonesia (36 islands), the Maluku Islands (11 islands), the Philippines (39 islands), and Melanesia (28 islands) (Fig. 1; see Table 1 for additional physical and geographic details). For each metacommunity, we compiled the presences and absences of all non-volant terrestrial mammal species on the included islands using checklists, atlases, and the literature (Table A1). All known introduced and domesticated species were omitted. Species lists for the Gulf of California, Japan, Indonesia, Philippines, and Mediterranean metacommunities were expanded from previously compiled datasets by Millien and Gonzalez (2011) and Millien-Parra and Jaeger (1999). Our selection of metacommunities and islands was limited by our ability to access complete species-level occurrence data for individual islands. See Table 2 for a summary of the mammalian biota included in each metacommunity.

Regional species pool

We assembled a regional species pool for each metacommunity, defined to include all terrestrial non-volant mammal species within 100km from any island coastline (see example, Fig. A1). We extracted all native, extant species whose distribution ranges extended within 100km from any

island coastline within the metacommunity. This 100km threshold was determined somewhat arbitrarily to include a portion of the mainland biota for each metacommunity, as well as mammal species present on islands that were not included in the metacommunity, but were geographically situated close to, or within the same island system. The same species pool definition was applied across all 9 metacommunities. We used terrestrial mammal distribution shapefiles from IUCN (2016), and island polygon shapefiles from Hijmans *et al.* (2010) in QGIS (QGIS Development Team 2016). See Table 2 for a summary of the mammalian biota included in each regional species pool.

Functional traits and phylogeny

For all species within the regional pools and metacommunities, we collected body size from Faurby *et al.* (2016), trophic level (i.e. herbivore, omnivore, or carnivore) from Kissling *et al.* (2014), and activity period (i.e. crepuscular, diurnal, or nocturnal) and foraging layer (i.e. ground level, scansorial, or arboreal) from Wilman *et al.* (2014). These traits were selected to characterize the spatial and temporal axes of species' ecological niches, and due to their relatively complete availability for the 930 included mammal species. When body size data was missing, it was completed using the literature when possible (9 species; see Table A2), and we otherwise took the mean of body size values for all available congeneric species. We also estimated species' climate niche limits based on their geographic distribution, in order to reflect whether they could survive within the island climates. We extracted the minimum and maximum annual mean temperature and annual precipitation, as well as the maximum temperature and precipitation seasonality from WorldClim version 1.4 (Hijmans *et al.* 2005) within each species' distributional range as delimited by IUCN (2016), using QGIS (QGIS Development Team 2016).

All phylogenetic analyses were conducted using Fritz *et al.* (2009)'s mammalian phylogeny, pruned to each metacommunity. Species that were not found in the tree were added to the root of their genus using the R package *phytools* (Revell 2012). When the genus was not within the tree, as was the case for *Musseromys*, *Paulamys*, and *Soricomys*, species were added to the tree at nodes shared by their closest relative genus, as designated by Fabre *et al.* (2016) and the Integrated Taxonomic Information System (ITIS).

β-diversity patterns

β-diversity can be partitioned into turnover and nestedness components, which respectively represent species replacement between sites (i.e. 'true' turnover) and species loss between sites due to differences in species richness (i.e. nestedness) (Baselga 2010). Here, we consider only the turnover component of β-diversity, as we are primarily interested in understanding the drivers of species replacement along spatial and environmental gradients (Baselga 2010). For each metacommunity, we quantified the taxonomic, functional, and phylogenetic turnover between island communities to identify the ecological and evolutionary drivers of community assembly.

Taxonomic turnover between island communities was measured using Simpson pairwise dissimilarity ($T\beta_{Sim}$), which measures species replacement independently of species richness (Baselga 2010). For the sake of comparison with previous studies on β-diversity, we include taxonomic turnover, despite its lack of sensitivity to ecological or evolutionary differentiations between species (Pavoine & Bonsall 2011).

To quantify functional turnover ($F\beta_{Sim}$), we adapted Villéger *et al.* (2013)'s approach for the use of one quantitative trait. Body size was chosen because it is a powerful descriptor of how mammals acquire energy, survive, reproduce, and grow, therefore encompasses multiple axes of mammalian niches in one trait (Western 1979; Lindstedt *et al.* 1986; Brown *et al.* 2004; Cardillo *et al.* 2005; Fritz *et al.* 2009; Smith & Lyons 2011). Body size was also the most completely collected trait across all metacommunity trait datasets, reducing the potential influence of trait interpolations on our assessment of $F\beta_{Sim}$. Based on the magnitude of overlap in body size range between communities, we compute $F\beta_{Sim}$ as:

$$F\beta_{Sim} = \frac{min\,(b,c)}{min(b,c) + a}$$

where a is the overlapping range in body size values between both communities, b is the range of body sizes that occur in the first community but not the second, and c is the range of body sizes that occur in the second community but not the first. Patterns of $F\beta_{Sim}$ along spatial and environmental gradients directly reflect the ecological processes that determine whether species can successfully occupy local niches, according to their functional traits.

Phylogenetic turnover ($P\beta_{Sim}$) was assessed using Leprieur *et al.* (2012)'s approach to partitioning phylogenetic β-diversity, which is based on the lengths of shared branches shared

between communities, and the lengths of branches unique to either of the two communities. As a result, $P\beta_{Sim}$ quantifies the replacement of unique lineages between communities, independently of differences in phylogenetic diversity (Leprieur *et al.* 2012). $P\beta_{Sim}$ patterns provide insight into how both ecological and evolutionary mechanisms influence community assembly, because they incorporate variation in phylogenetically-conserved traits between communities, as well as their evolutionary histories (Pavoine & Bonsall 2011). $P\beta_{Sim}$ therefore sheds light on how evolutionary processes like trait evolution and speciation influence diversity patterns along environmental and spatial gradients (Graham & Fine 2008; Cavender-Bares *et al.* 2009), complimenting the purely ecological insight given by $F\beta_{Sim}$. Using all three dimensions of turnover (taxonomic, functional, and phylogenetic) has the potential to highlight ecological and evolutionary responses to dispersal limitation and environmental filtering, providing a more integrated view of community assembly in these island metacommunities (Pavoine & Bonsall 2011).

We used a null model approach to control for sampling effects related to differences in species pool diversity, which allows the comparison of β-diversity patterns between different biogeographic regions (Gotelli & Graves 1996; Chase & Myers 2011; Lessard *et al.* 2012; Tucker *et al.* 2015). We simulated metacommunities by randomly sampling species from two definitions of the species pool: (1) the observed metacommunity, and (2) the regional pool, comprised of all species within 100km of any coastline. For the first null model, we used an independent-swap algorithm to randomly shuffle species occurrences throughout the metacommunity while conserving overall species frequencies (i.e. the number of islands occupied by each species) across the metacommunity, and local species richness for each island. For the second, we randomly sampled species from the regional pool while maintaining total species richness within the metacommunity, and local species richness for each island.

From 999 iterations of each null model, we computed the standardized effect size ($SES.\beta_{Sim}$) of taxonomic, functional, and phylogenetic β_{Sim} as the difference between observed β_{Sim} and mean expected β_{Sim}, divided by the standard deviation of expected β_{Sim} (Myers *et al.* 2013). Standardized effect sizes quantify the magnitude and direction of the difference in turnover patterns after accounting for species pool diversity, and are therefore a useful tool to compare how β-diversity patterns differ between metacommunities in different biogeographic regions (Gotelli & Graves 1996; Chase *et al.* 2011; Lessard *et al.* 2012). Turnover is higher than expected if $SES.\beta_{Sim}$ is positive, and is lower than expected if $SES.\beta_{Sim}$ is negative. When

SES.β_{Sim} values are different from 0, niche-based processes play a strong role in structuring communities, whereas null SES.β_{Sim} values indicate that turnover patterns result from neutral processes related to attributes of the species pool (Chase & Myers 2011; Lessard *et al.* 2012). The standardized effect sizes of taxonomic, functional, and phylogenetic turnover patterns computed using the first null model (i.e. accounting for sampling effects related to metacommunity structure) will be referred to as $SES_{META}T\beta_{Sim}$, $SES_{META}F\beta_{Sim}$, $SES_{META}P\beta_{Sim}$ respectively, while those computed using the second null model (i.e. accounting for sampling effects related to regional pool structure) will be referred to as $SES_{POOL}T\beta_{Sim}$, $SES_{POOL}F\beta_{Sim}$, $SES_{POOL}P\beta_{Sim}$.

Variation partitioning

We used variation partitioning to determine the relative influence of dispersal and environmental filtering on turnover patterns. For each metacommunity, we partitioned taxonomic, functional, and phylogenetic β_{Sim}, $SES_{META}\beta_{Sim}$, and $SES_{POOL}\beta_{Sim}$ into fractions of variation that are explained [a] purely by environmental variables (i.e. environmental filtering), [b] jointly by spatial and environmental variables (i.e. spatially-structured environmental filtering), [c] purely by spatial variables (i.e. dispersal), and [d] variation unexplained by the included spatial and environmental variables (Borcard *et al.* 1992; Legendre *et al.* 2005; Peres-Neto *et al.* 2006).

Environmental variables included topographic variables (island area, maximum elevation) and climatic variables (annual mean temperature, temperature seasonality, annual precipitation, and precipitation seasonality) from Weigelt *et al.* (2013), chosen to reflect the physical and climatic niche space available on each island (MacArthur & Wilson 1963; Whittaker *et al.* 2008; Weigelt *et al.* 2013). We log-transformed island area and maximum elevation, and centered and standardized all environmental variables. Collinear variables were removed sequentially according to variance inflation factors (VIF), using VIF = 3 as a threshold (Zuur *et al.* 2010). To represent the multiscale spatial distances between islands, we computed distance-based Moran's eigenvector maps (dbMEMs) using island coordinates from Weigelt *et al.* (2013) (Borcard & Legendre 2002; Legendre & Legendre 2012). Only positive dbMEMs were conserved in order to represent the effect of positive spatial autocorrelation on β-diversity patterns, because islands are expected to be more similar in community composition when they are closer in space, due to higher dispersal (Borcard & Legendre 2002). The dbMEMs were forward-selected following

Blanchet *et al.* (2008) when they significantly explained turnover within the metacommunity. See Table A4 for the spatial and environmental variables used in the following analyses for each metacommunity.

A distance-based redundancy analysis (db-RDA) was first carried out on taxonomic, functional, and phylogenetic β_{Sim}, $SES_{META}\beta_{Sim}$, $SES_{POOL}\beta_{Sim}$ to determine how much turnover was explained by spatial and environmental variables as a whole. Variation partitioning was then conducted to decompose the total explained variation into fractions of variation explained separately by [a] environmental variables, by [b] spatially structured environmental variation, and by [c] the dbMEMs (Legendre *et al.* 2005). The statistical significance of each fraction was assessed using permutation tests with 999 iterations with the anova.cca() function in *vegan* (Oksanen *et al.* 2007). However, fraction [b], i.e. the fraction of turnover explained by spatially-structured environmental filtering, could not be tested for significance, as it is obtained by subtracting the R_{adj} values of each explanatory matrix (i.e. either [a+b] or [b+c]) from that of the full model ([a+b+c]), and is therefore not a direct measure of variance (Legendre & Legendre 2012). Fraction [b]'s pseudo-R_{adj} can also be negative due to the additive property of its calculation, which signifies that environmental and spatial variables explain β-diversity better when considered together, rather than as summed individual effects (Legendre & Legendre 2012). Negative R_{adj} values for other fractions were interpreted as 0, meaning the selected variables do not meaningfully explain turnover patterns (Legendre & Legendre 2012).

Functional dispersion of the regional species pool

The functional dispersion (FDis) of each regional species pool was computed as the mean distance of individual species to the centroid of the metacommunity in multidimensional trait space (Laliberté & Legendre 2010). Here, trait space was defined using body size, trophic level, activity layer, foraging strata, and climatic niche limit estimations. We chose FDis because it is independent of species richness, which allows comparisons between regional species pools with differences in species diversity (Laliberté & Legendre 2010). FDis was computed using dbFD() in the R package *FD* (Laliberté 2011).

We then computed Pearson correlations between FDis of the regional species pool and the R_{adj} values of all communities for each fraction of explained turnover ([a], [b], [c], and [a+b+c])

to test whether the functional diversity available within the pool influences the relative strength of dispersal limitation and environmental filtering. Metacommunities were excluded if the total amount of variation explained by environment and space was negative (i.e. interpreted at 0). For significant correlations, we used linear regressions to describe the relationship between FDis and the strength of assembly processes, measured as the adjusted-R^2 of each fraction obtained from variation partitioning.

RESULTS

Strength of species sorting

Dispersal shaped turnover patterns in several metacommunities, while environmental filtering only acted on turnover patterns in conjunction with space. However, the strength of species sorting processes in structuring taxonomic, functional, and phylogenetic turnover differed widely across metacommunities, and across geographic regions.

Together, dispersal and environmental filtering significantly explained $T\beta_{Sim}$ in 4 metacommunities: Melanesia (R_{adj} = 0.41, p = 0.003), the Alexander Archipelago (R_{adj} = 0.36, p = 0.001), the Philippines (R_{adj} = 0.34, p = 0.003), and Indonesia (R_{adj} = 0.17, p = 0.02) (Fig. 2a; Table 3). However, dispersal ([c]) significantly structured $T\beta_{Sim}$ only in Melanesia (R_{adj} = 0.32, p = 0.001), the Alexander Archipelago (R_{adj} = 0.22, p = 0.001), and Indonesia (R_{adj} = 0.14, p = 0.01), while environmental filtering did not explain $T\beta_{Sim}$ in any metacommunity (Fig. 2a; Table 3). However, both $SES_{META}T\beta_{Sim}$ and $SES_{POOL}T\beta_{Sim}$ were universally unexplained by the included environmental and spatial variables (Fig. 4a, 5a). These large amounts of unexplained variation are expected, as $T\beta_{Sim}$ was identical to the expectations of the first null model, meaning taxonomic β-diversity was due to random sampling effects related to metacommunity structure, rather than niche-based processes (Fig. A5, A6; Table A3). Dispersal limitation and environmental filtering therefore did not structure taxonomic turnover in any metacommunity.

Environmental filtering and dispersal significantly explained $F\beta_{Sim}$ in the Philippines (R_{adj} = 0.48, p = 0.01) and in the Alexander Archipelago (R_{adj} = 0.31, p = 0.03), although dispersal ([c]) explained most of this variation (Phl: R_{adj} = 0.33, p = 0.02; Alx: R_{adj} = 0.29, p = 0.02) (Fig. 2b; Table 3). However, these patterns were not robust to random sampling effects from the

metacommunity and the regional pool. In the Philippines, explained variation in $SES_{META}F\beta_{Sim}$ (Fig. 3b; Table 4; $R_{adj} = 0.027$, $p = 0.05$) and in $SES_{POOL}F\beta_{Sim}$ (Fig. 4b; Table 5; $R_{adj} = 0.03$, $p = 0.03$) remained significant though very small, and dispersal ([c]) no longer explained variation significantly as a separate fraction. In the Alexander Archipelago, neither environmental filtering nor dispersal significantly explained $SES_{META}F\beta_{Sim}$ and $SES_{POOL}F\beta_{Sim}$. This implies that random sampling effects related to metacommunity and regional pool structure largely drove functional turnover patterns, rather than species sorting processes.

Phylogenetic turnover responded more strongly to environmental and spatial variation within most metacommunities. $P\beta_{Sim}$ was significantly structured by environmental and spatial variables as a whole in Melanesia ($R_{adj} = 0.49$, $p = 0.03$), the Gulf of California ($R_{adj} = 0.31$, $p = 0.04$), Indonesia ($R_{adj} = 0.12$, $p = 0.03$), and the Alexander Archipelago ($R_{adj} = 0.12$, $p = 0.03$) (Fig. 2c; Table 3). Environmental filtering ([a]) significantly explained a large portion of $P\beta_{Sim}$ in the Gulf of California ($R_{adj} = 0.25$, $p = 0.05$) (Fig. 2c; Table 3), although not after accounting for metacommunity and regional pool sampling effects (Fig. 3c, 4c; Table 4, 5). Dispersal limitation ([c]) significantly structured $P\beta_{Sim}$ in Indonesia ($R_{adj} = 0.15$, $p = 0.03$) and in the Alexander Archipelago ($R_{adj} = 0.06$, $p = 0.04$) (Fig. 2c; Table 3), though this pattern was also highly sensitive to random sampling effects (Fig. 3c, 4c; Table 4, 5). In Melanesia, a large portion of $P\beta_{Sim}$ was explained by spatially-structured environmental filtering (Fig. 2c; Table 3; [b] = 0.26), though environmental and spatial variables did not explain $P\beta_{Sim}$ when considered independently. Environment and space explained more phylogenetic turnover in the Melanesia metacommunity after accounting for sampling effects, accounting for over half of the variation in $SES_{META}P\beta_{Sim}$ (Fig. 3c; Table 4; $R_{adj} = 0.56$, $p = 0.13$) and in $SES_{POOL}P\beta_{Sim}$ (Fig. 4c; Table 5; $R_{adj} = 0.53$, $p = 0.004$), though not significantly for the former. Dispersal ([c]) significantly structured a large portion of Melanesia's $SES_{POOL}P\beta_{Sim}$ (Fig. 4c; Table 5; $R_{adj} = 0.24$, $p = 0.04$), and spatially-structured environmental filtering [b] explained a similarly large portion of $SES_{POOL}P\beta_{Sim}$ (Fig. 4c; Table 5; [b] = 0.25). In Indonesia, dispersal and environmental filtering also structured phylogenetic turnover more strongly after accounting for sampling effects of the regional pool (Fig. 4c; Table 5; $R_{adj} = 0.33$, $p = 0.001$). Dispersal was responsible for a moderate fraction of explained variation in both $P\beta_{Sim}$ and $SES_{POOL}P\beta_{Sim}$ ($P\beta_{Sim}$: $R_{adj} = 0.15$, $p = 0.004$; $SES_{POOL}P\beta_{Sim}$: $R_{adj} = 0.14$, $p = 0.01$), and spatially-structured environmental filtering significantly explained a similarly moderate fraction of $SES_{POOL}P\beta_{Sim}$ (Fig. 4c; Table 5; [b] = 0.14). This suggests that

dispersal limitation played a particularly important role in shaping the phylogenetic structure of the Melanesia and Indonesia metacommunities, independently of sampling effects at the regional pool level.

Functional dispersion of the regional species pool

Functional dispersion (FDis) varied across regional species pools, although this variation was not related to the relative importance of dispersal and environmental filtering in different metacommunities. The Gulf of California metacommunity had the least functionally dispersed regional species pool (FDis = 0.25), while the Adriatic Sea (FDis = 0.31) and the Mediterranean Sea regional species pools (FDis = 0.31) showed the highest levels of functional dispersion (Fig. 5). Despite being the most species-rich (Table 2), the Southeast Asian regional species pools showed relatively low levels of FDis (Fig. 5).

We expected a positive correlation between the strength of environmental filtering and the functional diversity of the species pool, as greater availability of functional traits within the pool should allow community composition to respond more strongly to environmental gradients. However, FDis was not correlated with the strength of environmental filtering ([a]) in any measures of β-diversity. Pearson correlations revealed that FDis was positively correlated with [b], the fraction of variation related to spatially-structured environmental filtering, in terms of $T\beta_{Sim}$ (Table 6; df = 6, $R = 0.80$, $p = 0.02$) and $F\beta_{Sim}$ (Table 6; df = 6, $R = 0.77$, $p = 0.02$). The relationship between FDis and $T\beta_{Sim}$ followed a positive linear trend (Fig. 6a; df = 6, $R_{adj} = 0.58$, $p = 0.018$, slope = 7.62, intercept = -2.06), as did the relationship between FDis and $F\beta_{Sim}$ (Fig. 6b; df = 6, $R_{adj} = 0.54$, $p = 0.023$, slope = 6.97, intercept = -2.02). This indicates that metacommunities that recruit species from more functionally diverse regional pools might undergo stronger spatially-structured environmental filtering, which is reflected in taxonomic and functional turnover patterns, although this relationship was not robust to sampling effects. There is therefore no consistent positive relationship between the functional diversity available within the regional species pool and the strength of environmental filtering.

DISCUSSION

Species sorting processes

In the present study, we investigated the relative influence of dispersal and environmental filtering on taxonomic, functional, and phylogenetic β-diversity within 9 island metacommunities, distributed around the globe. The results of the variation partitioning analyses did not support our hypothesis that species sorting drives community assembly. Instead, we found that dispersal limitation accounted for the most turnover across metacommunities, while environmental filtering played a secondary role. In fact, environmental filtering only informed turnover patterns in conjunction with space, suggesting that dispersal limitation is an important assembly process in these island metacommunities. The influence of dispersal and spatially-structured environmental filtering was also particularly marked in phylogenetic turnover patterns, whereas taxonomic and functional turnover patterns were left either entirely or largely unexplained in most metacommunities after accounting for sampling effects. Dispersal has therefore likely influenced the spatial structure of the metacommunities in conjunction with evolutionary processes, such as adaptation and speciation. This suggests that the evolutionary histories of species are linked to dispersal dynamics within certain metacommunities, which could not be captured by taxonomic and functional turnover patterns (Pavoine & Bonsall 2011). However, dispersal limitation was only prevalent in 2 of the 9 metacommunities (i.e. Indonesia and Melanesia) after accounting for random sampling effects. The relative influence of dispersal and environmental filtering therefore differed greatly across metacommunities, contrary to our hypothesis that species sorting is a universal driver of community assembly across geographic regions.

Although we do not have the information about competition and source-sink dynamics to test whether the 9 metacommunities conform to the patch-dynamic or the mass-effects paradigms of metacommunity theory, the strong influence of dispersal limitation in Melanesia and Indonesia suggest that the neutral perspective might be more applicable to the assembly of these metacommunities (Hubbell 2001; Leibold *et al.* 2004). In fact, across all metacommunities, community structure did not respond to environmental gradients, meaning that the matching of species' functional traits to local environmental niches did not influence community assembly.

There were therefore no ecologically meaningful differences between island environments and between species' functional abilities to occupy local niches. Instead, community structure responded to spatial gradients in Melanesia and in Indonesia, suggesting that neutral dispersal dynamics play the primary role in shaping their community structure.

The prevalence of dispersal as an important mechanism of community assembly likely results from the nature of island metacommunities, where dispersal dynamics are weak due to high isolation. The ocean represents a strong dispersal barrier between local communities in this study system, as long-distance overwater dispersal is difficult or impossible for terrestrial non-volant mammal species (Heaney 1984). As a result, it is logical that spatial distance plays such an important role in structuring β-diversity patterns: immigration is the most challenging task during community assembly at this scale for these taxa. This is particularly relevant in oceanic island systems like Melanesia (Table 1), which depend entirely on immigration to establish a large portion of community composition (Lawlor 1986).

However, large portions of turnover were left unexplained by the included spatial and environmental variables across all three dimensions of diversity in many metacommunities, especially after correcting for sampling effects. In several cases, no turnover was explained by the included environmental and spatial variables, despite evidence from $SES_{META}\beta_{Sim}$ and $SES_{POOL}\beta_{Sim}$ computations that turnover patterns differed significantly from both null expectations (Table A3; Fig. A5, A6). This unexplained turnover could be attributed to a combination of factors, such as the influence of neutral processes other than dispersal limitation, like speciation and ecological drift (Hubbell 2001), and unmeasured environmental and spatial variables that are relevant for the system (Borcard *et al.* 1992; Legendre *et al.* 2005). Missing environment and spatial variables are likely to account for the most unexplained variation in metacommunities like the Maluku Islands and Japan, which responded weakly to spatial and environmental variation despite showing non-random turnover patterns (Table A3; Fig. A5, A6). Furthermore, although the purely spatial fraction ([c]) of explained variation is usually interpreted as the influence of dispersal limitation, it may also reflect the influence of niche-based filtering by unmeasured, spatially autocorrelated environmental variables (Legendre *et al.* 2005). Missing environmental variables could therefore be inflating the importance of neutral processes across metacommunities.

The three dimensions of turnover varied widely in the strength of their responses to spatial and environmental gradients. As expected, taxonomic turnover ($T\beta_{Sim}$, $SES_{META}T\beta_{Sim}$, $SES_{POOL}T\beta_{Sim}$) was the least informative measure of turnover, because taxonomy does not directly reflect ecological or evolutionary relationships between species (Pavoine & Bonsall 2011). Although functional turnover ($F\beta_{Sim}$, $SES_{META}F\beta_{Sim}$, $SES_{POOL}F\beta_{Sim}$) has the potential to reveal the influence of niche-based ecological processes in most metacommunities, functional turnover was only weakly related to spatial and environmental gradients. These weak relationships might indicate that our measure of functional turnover was not sensitive enough to capture the variation in species' ecological niches between communities. We computed functional turnover patterns using one body size value per species, ignoring intraspecific variation that can be especially relevant for island mammals, for which body size varies from that of their mainland counterparts according to environmental factors like island area (Lomolino 1985; Millien & Gonzalez 2011). As a result, the functional turnover patterns we observed neglected a portion of communities' functional response to environmental variation between islands. Incorporating intraspecific variation would therefore provide a more sensitive measure of functional turnover, and thus improve our detection of environmental filtering. In contrast, phylogenetic turnover responded strongly to spatial and environmental gradients in some metacommunities ($P\beta_{Sim}$, $SES_{META}P\beta_{Sim}$, $SES_{POOL}P\beta_{Sim}$), signaling the potentially important role of evolutionary and ecological processes in community assembly.

In fact, the proposed paradigms of community assembly in metacommunity theory may not be well suited to these systems. Recently, the strictly ecological focus of metacommunity theory has been challenged in favour of considering the interaction between evolutionary and ecological processes (Loeuille & Leibold 2008; Hubert *et al.* 2015). As a result, the influence of dispersal and environmental filtering on community structure is slowly being considered in relation to adaptation and speciation at local and regional scales, though the nature of their effects in complex systems is still unclear (Loeuille & Leibold 2008; Hubert *et al.* 2015). For instance, in highly isolated communities where colonization is limited, rapid evolutionary rates can allow resident species to fill local niches despite being poorly suited to the environment, and might even result in the exclusion of functionally suitable species from the pool through priority effects (Loeuille & Leibold 2008; Mittelbach & Schemske 2015). The metacommunity framework is therefore being updated to incorporate dispersal limitation's non-linear influence on reproductive

isolation, and the selection of certain traits through environmental filtering that can further contribute to reproductive isolation (Hubert *et al.* 2015). While a united ecological and evolutionary perspective would greatly improve the metacommunity framework across all systems, considering evolutionary assembly processes would be especially important in island systems with high levels of endemism, such as those in South-East Asia (Kier *et al.* 2009), which encompass 4 of the 9 included metacommunities (i.e. Indonesia, Philippines, Maluku Islands, and Melanesia). For instance, we found that phylogenetic turnover responded most strongly to spatial and environmental gradients compared to functional and taxonomic turnover, especially in South-East Asia, though we did not evaluate the specific evolutionary mechanisms underlying these patterns. Focusing on dispersal and environmental filtering in a purely ecological context might therefore be simplifying community assembly, and neglecting a potentially important role of evolutionary processes that have structured community composition.

Unexplained variation may also be attributed to human activity, which has reshaped the taxonomic, functional, and phylogenetic composition of most included communities over thousands of years. The β-diversity patterns we have observed, and the relative importance of dispersal and environmental filtering, are likely to have been distorted by past human-related extinctions. In fact, human impacts have greatly altered mammalian body mass distributions worldwide (Santini *et al.* 2017), particularly on islands (Faurby *et al.* 2016), compared to historical patterns. For instance, humans drove endemic mammals to extinction and introduced species throughout the Mediterranean island system over several thousand years, thus strongly impacting the community structure we see today (Vigne 1992; Zeder 2008; Simmons 2012). As a result, the turnover patterns we observed in many metacommunities might poorly reflect the ecological and evolutionary processes governing community assembly due to human interference. Our findings should therefore be interpreted with this caveat in mind.

The role of the species pool

The functional diversity available within the species pool did not explain the variation in assembly processes across geographic regions. Although FDis of the pool was positively related to the influence of spatially-structured environmental filtering on observed taxonomic and functional turnover patterns, this relationship was not universal across measures of β-diversity

and was highly sensitive to sampling effects. There is therefore no evidence that the functional composition of the species pool determines the strength of species sorting at this scale.

However, our definition of the species pool was unfiltered (i.e. included all species within a defined region, regardless of dispersal abilities or environmental affinities), and was therefore not ecologically realistic, which could have impacted our ability to identify the neutral and niche-based processes that shaped our communities (Lessard *et al.* 2011). We also defined the pool identically across all metacommunities despite their varying levels of isolation (Table 1) and assumed this pool was equally available to all local communities within the network, which is an inaccurate depiction of the pool (Carstensen *et al.* 2013). For example, varying portions of mainland biota were included in the 100km buffer from island coastlines that was used to create the species pool, depending on the island system's distance from the mainland. This may have resulted in an underestimation of the extent of certain regional species pools, in particular for island systems that were distant from the mainland coastline. Our definition also ignored the spatial constraints that determine whether species can colonize the local communities, including differences in dispersal probabilities for islands with various degrees of isolation and variation in the included species' dispersal abilities (Lessard *et al.* 2012). Our definition also viewed species as ecologically equivalent, ignoring species' biological constraints such as the environmental affinities and biotic interactions that determine whether they are able to establish within the local communities (Lessard *et al.* 2012). In addition, our pool was static in both space and time, which omits the dynamic evolutionary and ecological processes shaping the pool across the spatial and temporal scales involved in community assembly (Cornell & Harrison 2014). For instance, speciation, immigration, and extinction processes shape the species pool dynamically over both ecological and evolutionary timeframes (Cornell & Harrison 2014). By constructing the species pool with contemporary island configuration and current mammalian distributions, which have been altered by human activity (Faurby *et al.* 2016; Santini *et al.* 2017), we are likely misrepresenting the functional composition of the pool during previous stages of community assembly that determined the bulk of community composition. Investigating the relationship between assembly processes and the functional composition of the pool according to definitions that differ in spatial and temporal extent might therefore reveal a relationship that we have missed by focusing on a single pool definition based on current-day species distributions.

Broader perspectives

In the present study, we assessed the role of the species pool's functional diversity in determining the relative influence of dispersal and environmental filtering on taxonomic, functional, and phylogenetic β-diversity patterns in 9 insular non-volant mammal metacommunities, distributed across the globe. We found that species sorting was not the prevalent mechanism of community assembly in any metacommunity, as dispersal limitation played a primary role in structuring functional and phylogenetic β-diversity. Colonization is therefore the major obstacle during the community assembly in some of the 9 insular mammal metacommunities. We therefore did not find a universal trend in the relative importance of dispersal and environmental filtering across metacommunities. The functional diversity available within the species pool was also not consistently related to the strength of species sorting.

The species-sorting model therefore does not explain community assembly in the majority of the 9 included metacommunities, suggesting that the model neglects important assembly processes. These findings raise questions about the ecological focus of the metacommunity framework, which ignores evolutionary processes like speciation and how they interact with dispersal dynamics and environmental filtering to influence community structure. Rather than focusing solely on how geographic isolation influences colonization from the species pool, it would be important to consider how geographic isolation results in reproduction isolation, which regulates adaptation and speciation rates and therefore the filling of local niches. Furthermore, niche-based processes like environmental filtering or biotic interactions should be addressed in relation to adaptation and speciation, which also contribute to the sorting of species into local environmental niches. More specifically, understanding how dispersal and niche-based processes interact with reproductive isolation at local and regional scales would provide much-needed insight into how species are added to local communities, and to the species pool at the regional scale. Incorporating evolutionary mechanisms into the metacommunity framework might thus allow us to ask more complex questions about interactions between the ecological and evolutionary drivers of community assembly, and better understand how biodiversity is created and maintained.

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TABLES

Table 1: Physical and geographic description of the 9 island metacommunities.

	n	Area (km^2)	Elevation (m)	Type		Dist (km)	Latitude (°)
				Land-bridge	Oceanic		
Adriatic	14	15 - 492	59 - 750	14	0	18	42.7 – 45.1
Alexander	51	1 - 7308	17 - 1575	51	0	45	54.8 – 59
California	18	1 - 1202	0 - 971	10	8	18	24.2 – 29.3
Indonesia	36	6 - 725098	21 - 3920	29	7	633	-9.2 – 7.3
Japan	6	2 - 227523	0 - 3671	5	1	548	30.6 – 36.7
Maluku	11	58 - 169021	356 - 3306	0	11	1270	-7.1 – 2.7
Mediterranean	35	2 - 25454	0 - 3237	12	23	115	35.5 – 43.4
Melanesia	28	1 - 35412	0 - 2641	5	23	983	-11.4 – -1.5
Philippines	39	10 - 104974	60 - 2804	5	34	1321	6 – 20.3

n = number of island communities; Island area = area (km^2) of the GADM island polygon (*www.gadm.org/version1*); Elevation = Range in maximum elevation (m) within the metacommunity; Type = number of islands of each island type (Land-bridge, i.e. islands connected to the mainland during the Last Glacial Maximum; Oceanic, i.e. islands that were not connected to the mainland during the Last Glacial Maximum; Dist = mean of the shortest great circle distance (km) between each island's mass centroid and the mainland coast within the metacommunity.

Table 2: Summary of the mammalian biota included in each metacommunity and regional species pool.

	Metacommunity			Regional species pool		
	sp	Orders	Mean body size (g)	sp	Orders	Mean body size (g)
Adriatic	15	5	107.2	67	7	207.7
Alexander	34	4	1182.3	54	5	594.4
California	33	4	119.4	105	7	195.6
Indonesia	124	8	517.6	324	14	497.3
Japan	44	6	235.1	45	7	636.0
Maluku	83	6	308.7	211	11	327.0
Mediterranean	21	6	308.6	71	7	269.2
Melanesia	34	4	336.7	237	8	322.1
Philippines	206	11	310.0	278	12	387.87

sp = total number of species, Orders = number of mammalian Orders represented in the metacommunity or regional species pool; Mean body size (g) = mean body size across all mammal species included in either the metacommunity or regional species pool, measured in grams.

Table 3: Variation partitioning of observed taxonomic, functional, and phylogenetic turnover (β_{Sim}) into fractions of variation explained [a] purely by environmental filtering, [b] by spatially-structured environmental filtering, [c] purely by dispersal, and [d] unexplained variation for each metacommunity.

			$T\beta_{Sim}$			$F\beta_{Sim}$			$P\beta_{Sim}$	
	Fraction	df	R_{adj}	p	df	R_{adj}	p	df	R_{adj}	p
Adriatic Sea	[a+b+c]	7	-0.104	0.97	7	0.228	0.29	7	0.170	0.33
	[a]	4	-0.049	0.74	4	0.190	0.29	4	0.346	0.20
	[b]	0	0.008	-	0	0.268	-	0	-0.630	-
	[c]	3	-0.063	0.81	3	-0.229	0.69	3	0.455	0.16
	[d]	-	1.104	-	-	0.772	-	-	0.830	-
Alexander Archipelago	[a+b+c]	**12**	**0.362**	**0.001**	**8**	**0.312**	**0.03**	**7**	**0.115**	**0.03**
	[a]	5	-0.044	0.94	5	-0.049	0.68	5	-0.037	0.77
	[b]	0	0.185	-	0	0.071	-	0	0.095	-
	[c]	**7**	**0.221**	**0.001**	**3**	**0.289**	**0.02**	**2**	**0.057**	**0.04**
	[d]	-	0.638	-	-	0.688	-	-	0.885	-
Gulf of California	[a+b+c]	7	0.231	0.06	7	0.338	0.07	**7**	**0.309**	**0.04**
	[a]	4	0.151	0.13	4	0.336	0.06	4	0.254	0.05
	[b]	0	-0.126	-	0	-0.174	-	0	-0.047	-
	[c]	3	0.206	0.07	3	0.177	0.09	3	0.101	0.25
	[d]	-	0.769	-	-	0.662	-	-	0.691	-
Indonesia	[a+b+c]	**13**	**0.167**	**0.02**	13	0.152	0.14	**13**	**0.126**	**0.03**
	[a]	5	-0.075	0.94	5	0.115	0.13	5	-0.083	0.98
	[b]	0	0.103	-	0	0.014	-	0	0.062	-
	[c]	**8**	**0.139**	**0.01**	8	0.024	0.40	**8**	**0.148**	**0.004**
	[d]	-	0.833	-	-	0.848	-	-	0.874	-
Japan	[a+b+c]	5	0.142	0.35	5	-0.436	0.73	5	0.313	0.26
	[a]	3	-0.235	0.43	3	-0.197	0.58	3	-0.167	0.33
	[b]	0	0.432	-	0	0.150	-	0	0.864	-
	[c]	2	-0.055	0.51	2	-0.389	0.64	2	-0.384	0.51
	[d]	-	0.858	-	-	1.436	-	-	0.687	-
Maluku Islands	[a+b+c]	7	0.303	0.23	7	0.321	0.15	7	0.662	0.15
	[a]	4	0.232	0.40	4	0.428	0.20	4	0.437	0.17
	[b]	0	-0.225	-	0	-0.401	-	0	-0.050	-
	[c]	3	0.297	0.36	3	0.294	0.33	3	0.274	0.25
	[d]	-	0.697	-	-	0.679	-	-	0.338	-
Mediterranean	[a+b+c]	5	0.156	0.07	7	0.085	0.30	7	-0.062	0.63
	[a]	4	0.008	0.49	4	-0.038	0.59	4	-0.191	0.95
	[b]	0	0.167	-	0	0.002	-	0	0.072	-
	[c]	1	-0.019	0.68	3	0.121	0.15	3	0.057	0.28

	[d]	-	0.844	-	-	0.915	-	-	1.062	-
Melanesia	[a+b+c]	**8**	**0.406**	**0.001**	9	0.287	0.14	**9**	**0.492**	**0.03**
	[a]	5	-0.005	0.48	4	0.056	0.35	4	0.028	0.37
	[b]	0	0.093	-	0	-0.150	-	0	0.255	-
	[c]	**3**	**0.318**	**0.001**	5	0.382	0.06	5	0.208	0.08
	[d]	-	0.594	-	-	0.713	-	-	0.508	-
Philippines	[a+b+c]	**14**	**0.338**	**0.003**	**14**	**0.476**	**0.01**	14	-0.106	0.74
	[a]	5	0.048	0.19	5	0.138	0.17	5	-0.068	0.71
	[b]	0	0.169	-	0	0.007	-	0	0.058	-
	[c]	9	0.120	0.07	**9**	**0.331**	**0.02**	9	-0.096	0.72
	[d]	-	0.662	-	-	0.524	-	-	1.106	-

Fraction [a+b+c] = total variation explained by environmental filtering and dispersal, [a] = variation explained purely by environmental filtering, [b] = variation explained by spatially-structured environmental filtering, [c] = variation explained purely by dispersal, [d] = residuals; df = degrees of freedom for each fraction; R_{adj} = adjusted R^2 for each fraction (note: R_{adj} for the [b] fraction is a pseudo-R_{adj}, obtained from subtraction); p: p-value describing the significance of each fraction of explained variation. Significant fractions ($p \leq 0.05$) are bolded.

Table 4: Variation partitioning of the standardized effect size of taxonomic, functional, and phylogenetic turnover under random sampling of the metacommunity ($SES_{META}\beta_{Sim}$), into fractions of variation explained [a] purely by environmental filtering, [b] by spatially-structured environmental filtering, [c] purely by dispersal, and [d] unexplained variation for each metacommunity.

		$SES_{META}T\beta_{Sim}$			$SES_{META}F\beta_{Sim}$			$SES_{META}P\beta_{Sim}$		
	Fraction	df	R_{adj}	p	df	R_{adj}	p	df	R_{adj}	p
Adriatic Sea	[a+b+c]	7	0.027	0.36	**7**	**0.119**	**0.03**	7	0.011	0.42
	[a]	4	0.036	0.35	4	0.125	0.07	4	-0.003	0.52
	[b]	0	0.010	-	0	-0.011	-	0	-0.004	-
	[c]	3	-0.020	0.59	3	0.005	0.48	3	0.019	0.42
	[d]	-	0.973	-	-	0.881	-	-	0.989	-
Alexander Archipelago	[a+b+c]	12	-0.005	0.86	8	0.001	0.35	7	-0.007	0.99
	[a]	5	-0.002	0.69	5	0.000	0.47	5	-0.005	0.93
	[b]	0	-0.005	-	0	-0.001	-	0	-0.002	-
	[c]	7	0.002	0.40	3	0.001	0.35	2	0.000	0.57
	[d]	-	1.005	-	-	0.999	-	-	1.007	-
Gulf of California	[a+b+c]	7	-0.013	0.64	7	0.096	0.05	7	-0.024	0.74
	[a]	4	-0.023	0.68	4	0.113	0.05	4	-0.017	0.62
	[b]	0	0.026	-	0	-0.076	-	0	-0.017	-
	[c]	3	-0.016	0.64	3	0.058	0.16	3	0.010	0.45
	[d]	-	1.013	-	-	0.904	-	-	1.024	-
Indonesia	[a+b+c]	13	-0.030	0.99	13	0.012	0.16	13	-0.007	0.76
	[a]	5	-0.017	0.85	5	0.002	0.44	5	-0.008	0.69
	[b]	0	0.002	-	0	-0.006	-	0	0.009	-
	[c]	8	-0.015	0.84	8	0.016	0.18	8	-0.008	0.71
	[d]	-	1.030	-	-	0.988	-	-	1.007	-
Japan	[a+b+c]	5	-0.097	0.71	5	0.003	0.44	**5**	**0.294**	**0.05**
	[a]	3	-0.121	0.68	3	0.034	0.42	3	0.243	0.16
	[b]	0	0.047	-	0	0.007	-	0	-0.149	-
	[c]	2	-0.022	0.53	2	-0.038	0.52	2	0.200	0.24
	[d]	-	1.097	-	-	0.997	-	-	0.706	-
Maluku Islands	[a+b+c]	7	-0.378	0.89	7	-0.065	0.55	7	0.029	0.50
	[a]	4	-0.320	0.79	4	-0.144	0.63	4	-0.050	0.54
	[b]	0	0.173	-	0	0.183	-	0	-0.038	-
	[c]	3	-0.232	0.67	3	-0.104	0.60	3	0.118	0.45
	[d]	-	1.378	-	-	1.065	-	-	0.971	-
Mediterranean	[a+b+c]	5	0.071	0.36	7	0.001	0.44	7	-0.025	0.97
	[a]	4	-0.014	0.56	4	-0.009	0.73	4	-0.025	0.95
	[b]	0	-0.048	-	0	-0.014	-	0	-0.010	-

	[c]	1	0.133	0.16	3	0.024	0.09	3	0.010	0.25
	[d]	-	0.929	-	-	0.999	-	-	1.025	-
Melanesia	[a+b+c]	8	-0.041	0.97	9	-0.011	0.63	9	0.558	0.13
	[a]	5	0.000	0.52	4	0.005	0.47	4	0.153	0.25
	[b]	0	-0.021	-	0	-0.015	-	0	0.388	-
	[c]	3	-0.020	0.73	5	-0.001	0.54	5	0.018	0.33
	[d]	-	1.041	-	-	1.011	-	-	0.442	-
Philippines	[a+b+c]	14	-0.021	0.94	**14**	**0.027**	**0.05**	**14**	**0.026**	**0.03**
	[a]	5	-0.001	0.58	5	-0.006	0.60	5	0.020	0.25
	[b]	0	-0.004	-	0	0.008	-	0	-0.017	-
	[c]	9	-0.016	0.74	9	0.025	0.15	9	0.024	0.17
	[d]	-	1.021	-	-	0.973	-	-	0.974	-

Fraction [a+b+c] = total variation explained by environmental filtering and dispersal, [a] = variation explained purely by environmental filtering, [b] = variation explained by spatially-structured environmental filtering, [c] = variation explained purely by dispersal, [d] = residuals; df = degrees of freedom for each fraction; R_{adj} = adjusted R^2 for each fraction (note: R_{adj} for the [b] fraction is a pseudo-R_{adj}, obtained from subtraction); p: p-value describing the significance of each fraction of explained variation. Significant fractions ($p \leq 0.05$) are bolded.

Table 5: Variation partitioning of the standardized effect size of taxonomic, functional, and phylogenetic turnover under random sampling of the regional pool ($SES_{POOL}\beta_{Sim}$), into fractions of variation explained [a] purely by environmental filtering, [b] by spatially-structured environmental filtering, [c] purely by dispersal, and [d] unexplained variation for each metacommunity.

		$SES_{POOL}T\beta_{Sim}$			$SES_{POOL}F\beta_{Sim}$			$SES_{POOL}P\beta_{Sim}$		
	Fraction	df	R_{adj}	p	df	R_{adj}	p	df	R_{adj}	p
Adriatic Sea	[a+b+c]	7	0.092	0.07	7	-0.087	0.91	7	-0.168	0.92
	[a]	4	0.013	0.43	4	-0.068	0.76	4	-0.158	0.85
	[b]	0	0.010	-	0	0.073	-	0	0.134	-
	[c]	3	0.069	0.19	3	-0.092	0.83	3	-0.145	0.89
	[d]	-	0.908	-	-	1.087	-	-	1.168	-
Alexander Archipelago	[a+b+c]	12	-0.030	1.00	8	0.001	0.43	**8**	**0.076**	**0.02**
	[a]	5	-0.008	0.92	5	0.001	0.38	5	0.037	0.10
	[b]	0	-0.012	-	0	-0.002	-	0	0.011	-
	[c]	7	-0.011	0.97	3	0.002	0.29	3	0.029	0.08
	[d]	-	1.030	-	-	0.999	-	-	0.924	-
Gulf of California	[a+b+c]	7	-0.028	0.82	7	0.011	0.42	7	0.168	0.11
	[a]	4	-0.029	0.70	4	0.004	0.47	4	-0.007	0.50
	[b]	0	0.025	-	0	0.011	-	0	0.120	-
	[c]	3	-0.023	0.67	3	-0.004	0.53	3	0.055	0.28
	[d]	-	1.028	-	-	0.989	-	-	0.832	-
Indonesia	[a+b+c]	13	-0.050	1.00	13	0.014	0.16	**13**	**0.333**	**0.001**
	[a]	5	-0.016	0.83	5	0.009	0.28	5	0.058	0.08
	[b]	0	-0.004	-	0	-0.013	-	0	0.140	-
	[c]	8	-0.029	0.96	8	0.018	0.15	**8**	**0.135**	**0.01**
	[d]	-	1.050	-	-	0.986	-	-	0.667	-
Japan	[a+b+c]	5	-0.133	0.81	5	0.072	0.28	5	0.331	0.30
	[a]	3	-0.125	0.70	3	0.053	0.39	3	0.446	0.23
	[b]	0	-0.048	-	0	-0.020	-	0	0.153	-
	[c]	2	0.040	0.41	2	0.039	0.42	2	-0.268	0.98
	[d]	-	1.133	-	-	0.928	-	-	0.669	-
Maluku Islands	[a+b+c]	7	-0.160	0.71	7	-0.101	0.63	7	0.492	0.19
	[a]	4	-0.222	0.71	4	-0.194	0.70	4	0.514	0.18
	[b]	0	0.128	-	0	0.240	-	0	-0.427	-
	[c]	3	-0.066	0.59	3	-0.147	0.66	3	0.405	0.31
	[d]	-	1.160	-	-	1.101	-	-	0.508	-
Mediterranean	[a+b+c]	5	-0.028	1.00	7	-0.005	0.66	7	0.029	0.36
	[a]	4	-0.013	0.90	4	-0.003	0.59	4	0.022	0.34
	[b]	0	-0.019	-	0	-0.005	-	0	-0.025	-

	[c]	1	0.004	0.32	3	0.003	0.44	3	0.033	0.30
	[d]	-	1.028	-	-	1.005	-	-	0.971	-
Melanesia	[a+b+c]	8	-0.066	1.00	9	-0.014	0.63	**9**	**0.530**	**0.004**
	[a]	5	-0.006	0.55	4	-0.015	0.64	4	0.042	0.26
	[b]	0	-0.022	-	0	-0.010	-	0	0.249	-
	[c]	3	-0.038	0.88	5	0.011	0.40	**5**	**0.239**	**0.04**
	[d]	-	1.066	-	-	1.014	-	-	0.470	-
Philippines	[a+b+c]	14	-0.066	1.00	**14**	**0.030**	**0.03**	14	0.148	0.13
	[a]	5	-0.018	0.75	5	0.006	0.42	5	0.031	0.30
	[b]	0	-0.012	-	0	-0.003	-	0	0.016	-
	[c]	9	-0.037	0.92	9	0.027	0.15	9	0.100	0.15
	[d]	-	1.066	-	-	0.970	-	-	0.852	-

Fraction [a+b+c] = total variation explained by environmental filtering and dispersal, [a] = variation explained purely by environmental filtering, [b] = variation explained by spatially-structured environmental filtering, [c] = variation explained purely by dispersal, [d] = residuals; df = degrees of freedom for each fraction; R_{adj} = adjusted R^2 for each fraction (note: R_{adj} for the [b] fraction is a pseudo-R_{adj}, obtained from subtraction); p: p-value describing the significance of each fraction of explained variation. Significant fractions ($p \leq 0.05$) are bolded.

Table 6: Pearson correlations between FDis of the regional species pool and the amount of variation explained by spatially structured environmental variation, for observed turnover and standardized effect sizes computed from each null model.

β-diversity measure	df	R	t	CI	p
TβSim	**6**	**0.80**	**3.25**	**0.21, 0.96**	**0.02 ***
FβSim	**6**	**0.78**	**3.02**	**0.16, 0.96**	**0.02 ***
PβSim	5	0.02	0.05	-0.74, 0.76	0.96
SES_{META}TβSim	-	-	-	-	-
SES_{META}FβSim	4	-0.27	-0.56	-0.89, 0.69	0.61
SES_{META}PβSim	3	-0.55	-1.13	-0.96, 0.65	0.34
SES_{POOL}TβSim	-	-	-	-	-
SES_{POOL}FβSim	4	0.45	1.01	-0.57, 0.92	0.37
SES_{POOL}PβSim	6	0.06	0.14	-0.67, 0.73	0.89

df = degrees of freedom; R = Pearson correlation coefficient, t = test statistic, CI = 95% confidence interval for R, p = p-value (* $p < 0.05$). Significant correlations ($p < 0.05$) are bolded.

FIGURES

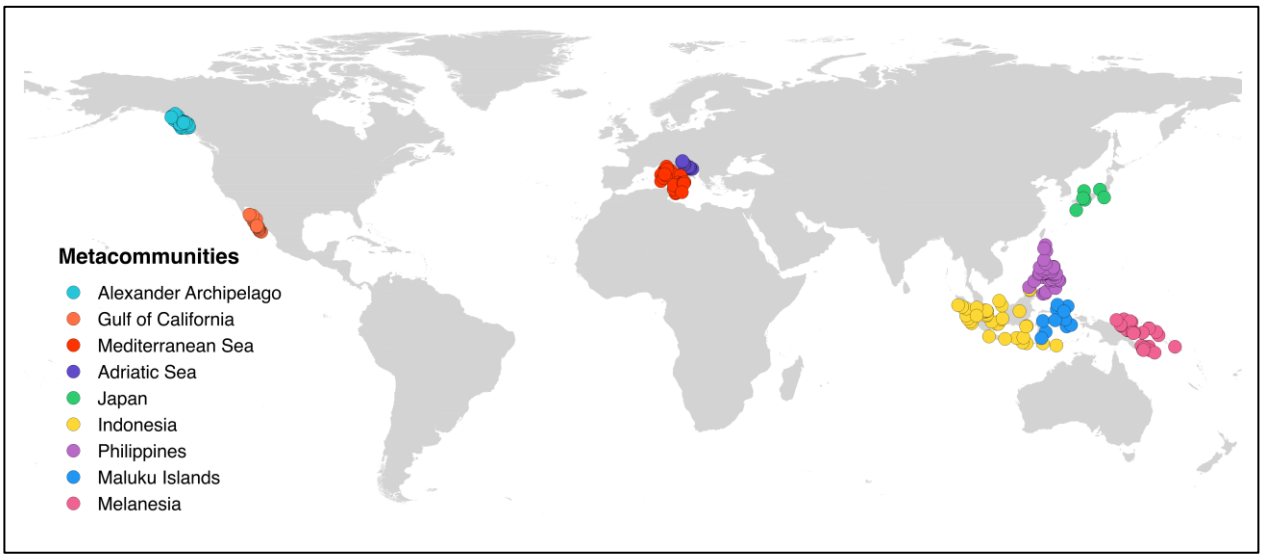

Figure 1: World map showing the locations of the 9 studied insular metacommunities, where each point represents a sampled island community, and colours differentiate metacommunities.

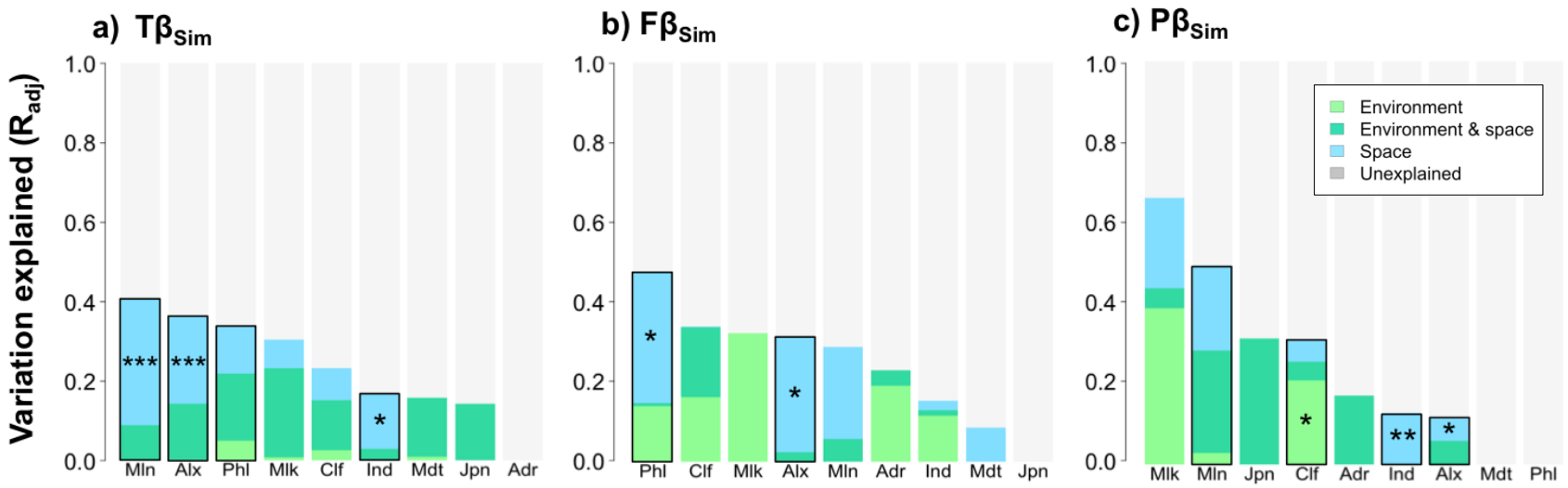

Figure 2: Fractions of variation in observed turnover explained by environmental and spatial variables in each metacommunity for (a) $T\beta_{Sim}$, (b) $F\beta_{Sim}$, and (c) $P\beta_{Sim}$. Solid border indicates significance of total variation explained by environment and space ($p \leq 0.05$). Asterisks indicate each testable fractions' significance: *** $p \leq 0.001$; ** $p < 0.01$, * $p \leq 0.05$. The metacommunities are abbreviated as: Adr = Adriatic Sea, Alx = Alexander Archipelago, Clf = Gulf of California, Jpn = Japan, Ind = Indonesia, Mdt = Mediterranean, Mlk = Maluku, Mln = Melanesia, Phl = Philippines.

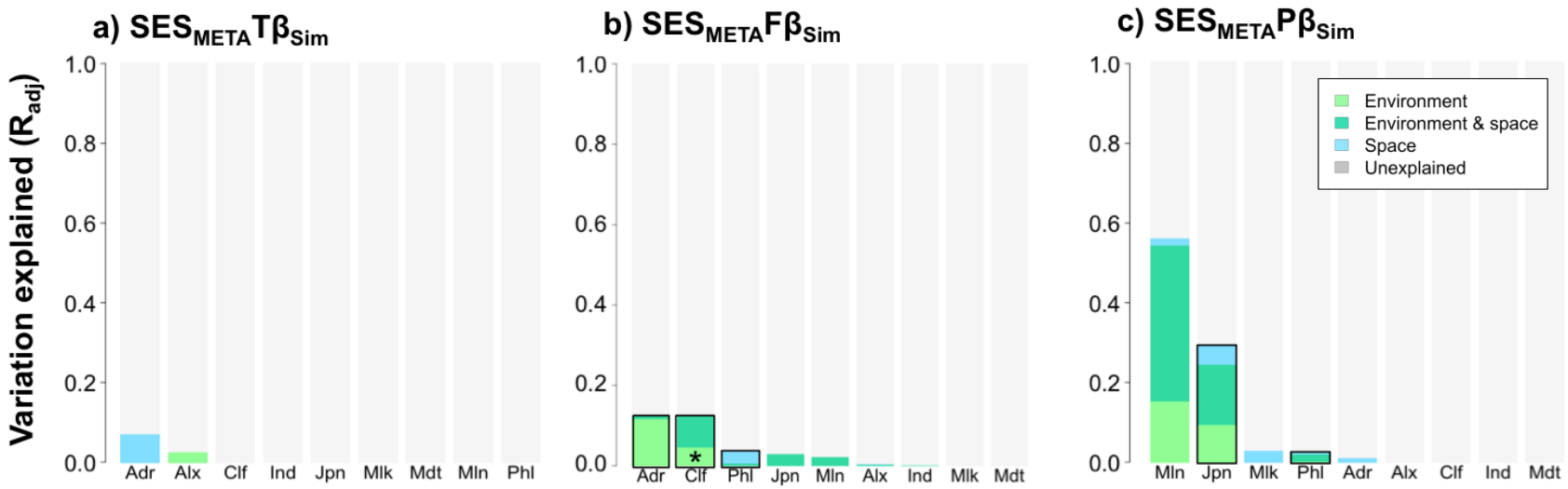

Figure 3: Variation in the standardized effect sizes of β-diversity under null model 1, explained by environmental and spatial variables in each metacommunity for (a) $SES_{META}T\beta_{Sim}$, (b) $SES_{META}F\beta_{Sim}$, and (c) $SES_{META}P\beta_{Sim}$. Solid border indicates significance of total variation explained by environment and space ($p \leq 0.05$). Asterisks indicate each testable fractions' significance: *** $p \leq 0.001$; ** $p < 0.01$, * $p \leq 0.05$. The metacommunities are abbreviated as: Adr = Adriatic Sea, Alx = Alexander Archipelago, Clf = Gulf of California, Jpn = Japan, Ind = Indonesia, Mdt = Mediterranean, Mlk = Maluku, Mln = Melanesia, Phl = Philippines.

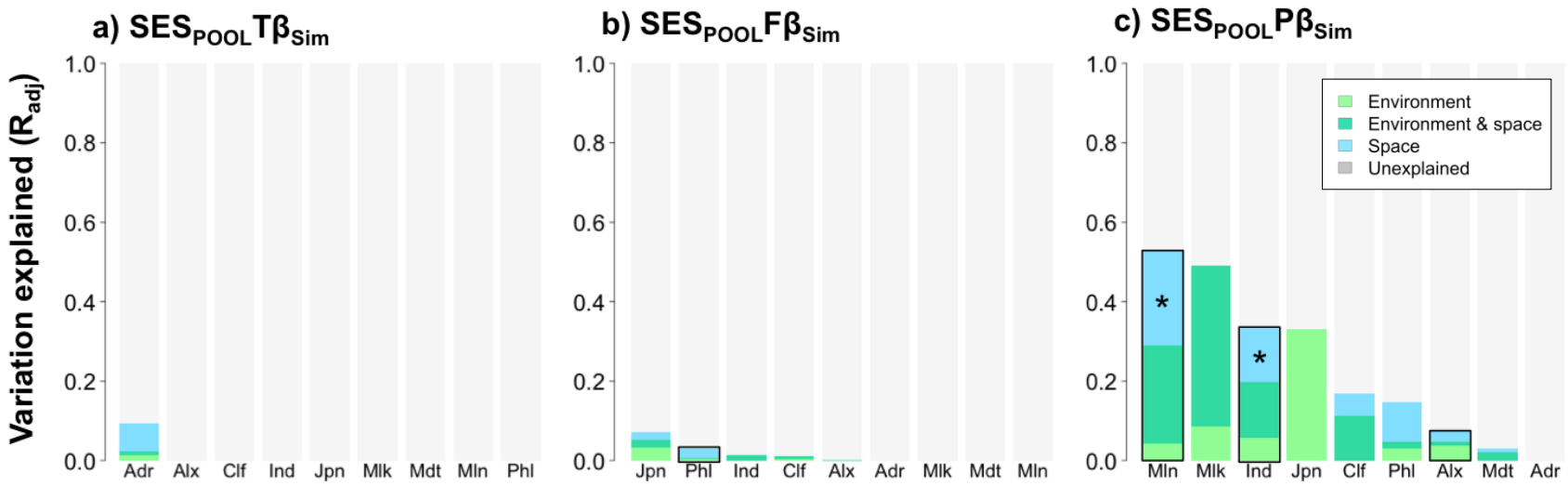

Figure 4: Variation in the standardized effect sizes of β-diversity under null model 2, explained separately and jointly by environmental and spatial variables in each metacommunity for (a) $SES_{POOL}T\beta_{Sim}$, (b) $SES_{POOL}F\beta_{Sim}$, and (c) $SES_{POOL}P\beta_{Sim}$. Solid border indicates significance of total variation explained by environment and space ($p \leq 0.05$). Asterisks indicate each testable fractions' significance: *** $p \leq 0.001$; ** $p < 0.01$, * $p \leq 0.05$. The metacommunities are abbreviated as: Adr = Adriatic Sea, Alx = Alexander Archipelago, Clf = Gulf of California, Jpn = Japan, Ind = Indonesia, Mdt = Mediterranean, Mlk = Maluku, Mln = Melanesia, Phl = Philippines.

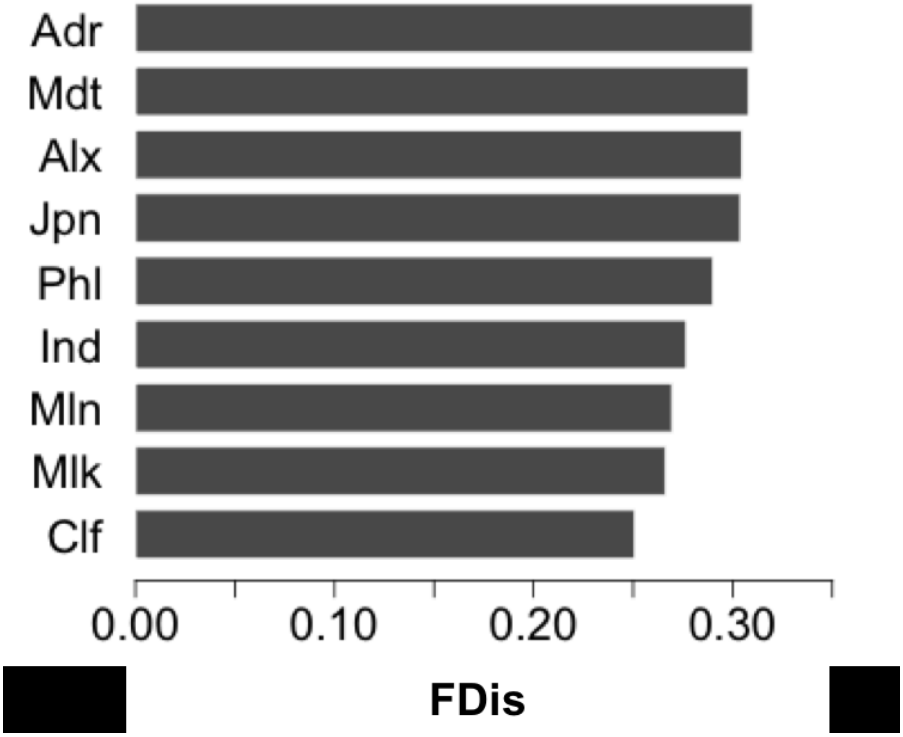

Figure 5: Functional dispersion (FDis) of the regional species pool for each metacommunity. The metacommunities are abbreviated as: Adr = Adriatic Sea, Alx = Alexander Archipelago, Clf = Gulf of California, Jpn = Japan, Ind = Indonesia, Mdt = Mediterranean, Mlk = Maluku, Mln = Melanesia, Phl = Philippines.

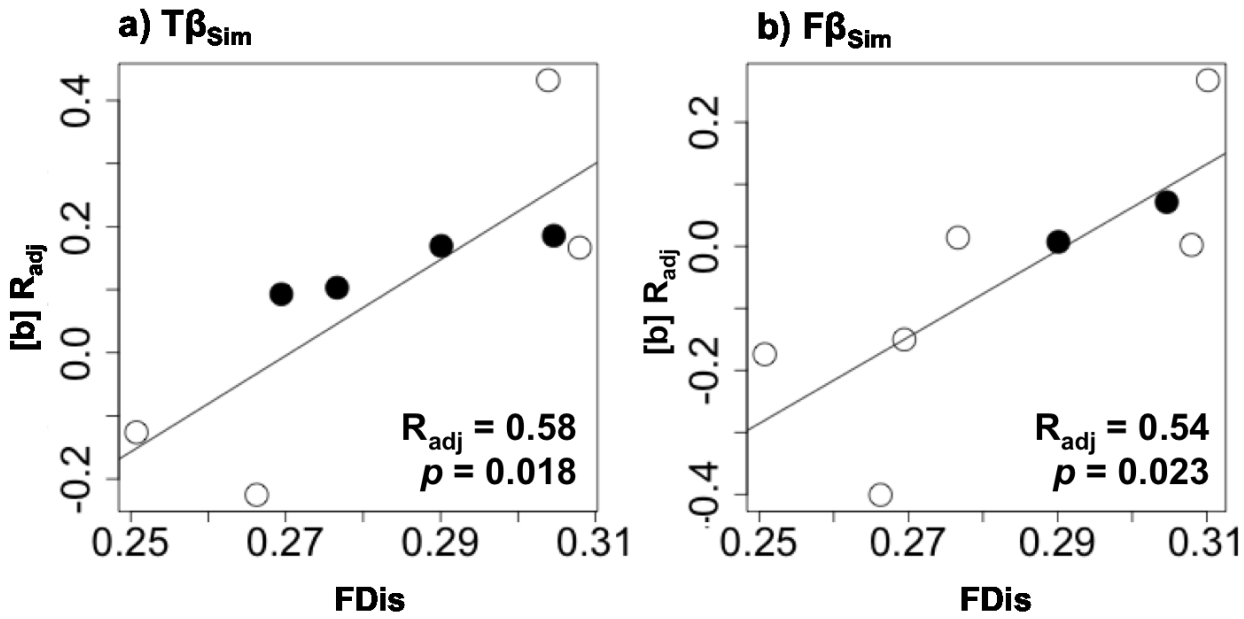

Figure 6: Relationship between the functional dispersion (FDis) of the regional species pool and the amount of turnover explained simultaneously by dispersal and environmental filtering ([b]). The solid line shows the linear regression modeling the relationship between FDis and pseudo-R_{adj}. Filled circles are metacommunities where the total amount of variation in β-diversity explained by environment and space was significant ($p \leq 0.05$). (a) Observed taxonomic turnover ($T\beta_{Sim}$): slope = 7.62, intercept = -2.06, df = 6, R_{adj} = 0.58, p = 0.018. (b) Observed functional turnover ($F\beta_{Sim}$): slope = 6.97, intercept = -2.02, df = 6, R_{adj} = 0.54, p = 0.023.

APPENDIX

Table A1: Sources of community composition data for each metacommunity.

Metacommunity	Data sources
Alexander Archipelago	Conroy, C.J., Demboski, J.R. & Cook, J.A. (1999). Mammalian biogeography of the Alexander Archipelago of Alaska: a north temperate nested fauna. *Journal of Biogeography*, 26, 343-352. Cook, J.A. & MacDonald, S. (2007). *Mammals and amphibians of Southeast Alaska*. MacDonald, S.O. & Cook, J.A. (2010). *Recent mammals of Alaska*. University of Alaska Press.
Adriatic Sea	Barun, A., Simberloff, D., Meiri, S., Tvrtković, N. & Tadić, Z. (2015). Possible character displacement of an introduced mongoose and native marten on Adriatic Islands, Croatia. *Journal of biogeography*, 42, 2257-2269. Krystufek, B. & Kletecki, E. (2007). Biogeography of small terrestrial vertebrates on the Adriatic landbridge islands. *Folia zoologica*, 56, 225. Kryštufek, B., Murariu, D. & Kurtonur, C. (1997). Present distribution of the Golden Jackal Canis aureus in the Balkans and adjacent regions. *Mammal Review*, 27, 109-114.
Gulf of California	Álvarez-Castañeda, S.T. & Ortega-Rubio, A. (2003). Current status of rodents on islands in the Gulf of California. *Biological Conservation*, 109, 157-163. Ceballos, G. (2014). *Mammals of Mexico*. JHU Press. IUCN (2016). The IUCN Red List of Threatened Species. Version 2016-3. Millien, V. & Gonzalez, A. (2011). The maximal body mass–area relationship in island mammals. *Journal of biogeography*, 38, 2278-2285.
Indonesia	Meijaard, E. (2003). Mammals of south- east Asian islands and their Late Pleistocene environments. *Journal of Biogeography*, 30, 1245-1257. Millien, V. & Gonzalez, A. (2011). The maximal body mass–area relationship in island mammals. *Journal of biogeography*, 38, 2278-2285. Suyanto, A., Yoneda, M., Maryanto, I., Maharadatunkamsi, H. & Sugardjito, J. (1998). Checklist of the mammals of Indonesia. *LIPI-JICA Joint Project for Biodiversity Conservation in Indonesia*.
Japan	Dobson, M. (1994). Patterns of distribution in Japanese land mammals. *Mammal Review*, 24, 91-111. IUCN (2016). The IUCN Red List of Threatened Species. Version 2016-3. Millien-Parra, V. & Jaeger, J.J. (1999). Island biogeography of the Japanese terrestrial mammal assemblages: an example of a relict fauna. *Journal of Biogeography*, 26, 959-972.

Maluku Islands	Meijaard, E. (2003). Mammals of south- east Asian islands and their Late Pleistocene environments. *Journal of Biogeography*, 30, 1245-1257. Millien, V. & Gonzalez, A. (2011). The maximal body mass–area relationship in island mammals. *Journal of biogeography*, 38, 2278-2285. Suyanto, A., Yoneda, M., Maryanto, I., Maharadatunkamsi, H. & Sugardjito, J. (1998). Checklist of the mammals of Indonesia. *LIPI-JICA Joint Project for Biodiversity Conservation in Indonesia*.
Mediterranean	Angelici, F., Laurenti, A. & Nappi, A. (2009). A checklist of the mammals of small Italian islands. *Hystrix, the Italian Journal of Mammalogy*, 20. Millien, V. & Gonzalez, A. (2011). The maximal body mass–area relationship in island mammals. *Journal of biogeography*, 38, 2278-2285. Vigne, J.-D. (1992). Zooarchaeology and the biogeographical history of the mammals of Corsica and Sardinia since the last ice age. *Mammal Review*, 22, 87-96.
Melanesia	Lavery, T.H., Olds, A.D., Seddon, J.M. & Leung, L.K.P. (2016). The mammals of northern Melanesia: speciation, ecology, and biogeography. *Mammal Review*, 46, 60-76.
Philippines	Heaney, L.R., Balete, D.S., Duya, M.R.M., Duya, M.V., Jansa, S.A., Steppan, S.J. *et al.* (2016). Doubling diversity: a cautionary tale of previously unsuspected mammalian diversity on a tropical oceanic island. *Frontiers of Biogeography*, 8. Heaney, L.R., Dolar, M.L., Balete, D.S., Esselstyn, J.A., Rickart, E.A. & Sedlock, J.L. (2010). Synopsis of Philippine Mammals. *The Field Museum of Natural History*. Heaney, L.R., Dolar, M.L., Balete, D.S., Esselstyn, J.A., Rickart, E.A. & Sedlock, J.L. (2011). Supplement to the Synopsis of Philippine Mammals. *The Field Museum of Natural History*. Meijaard, E. (2003). Mammals of south- east Asian islands and their Late Pleistocene environments. *Journal of Biogeography*, 30, 1245-1257. Millien, V. & Gonzalez, A. (2011). The maximal body mass–area relationship in island mammals. *Journal of biogeography*, 38, 2278-2285.

Table A2: Sources of body size data for species that were not found in Faurby *et al.* (2016).

Metacommunity	Species	Source
Indonesia	*Musseromys gulantang*	Heaney, L.R., Balete, D.S., Rickart, E.A., Veluz, M.J. & Jansa, S.A. (2014). Three new species of Musseromys (Muridae, Rodentia), the endemic Philippine tree mouse from Luzon Island.
Philippines	*Apomys iridensis*	Heaney, L.R., Balete, D.S., Veluz, M.J., Steppan, S.J., Esselstyn, J.A., Pfeiffer, A.W. *et al.* (2014). Two new species of Philippine forest mice (Apomys, Muridae, Rodentia) from Lubang and Luzon Islands, with a redescription of Apomys sacobianus Johnson, 1962. *Proceedings of the Biological Society of Washington*, 126, 395-413.
	Archboldomys maximus	Balete, D.S., Rickart, E.A., Heaney, L.R., Alviola, P.A., Duya, M.V., Duya, M.R.M. *et al.* (2012). Archboldomys (Muridae: Murinae) reconsidered: a new genus and three new species of shrew mice from Luzon Island, Philippines.
	Batomys uragon	Balete, D.S., Rickart, E.A., Heaney, L.R. & Jansa, S.A. (2015). A new species of Batomys (Muridae, Rodentia) from southern Luzon Island, Philippines. *Proceedings of the Biological Society of Washington*, 128, 22-39.
	Musseromys anacuao	Heaney, L.R., Balete, D.S., Rickart, E.A., Veluz, M.J. & Jansa, S.A. (2014). Three new species of Musseromys (Muridae, Rodentia), the endemic Philippine tree mouse from Luzon Island.
	Musseromys beneficus	Heaney, L.R., Balete, D.S., Rickart, E.A., Veluz, M.J. & Jansa, S.A. (2014). Three new species of Musseromys (Muridae, Rodentia), the endemic Philippine tree mouse from Luzon Island.
	Musseromys inopinatus	Heaney, L.R., Balete, D.S., Rickart, E.A., Veluz, M.J. & Jansa, S.A. (2014). Three new species of Musseromys (Muridae, Rodentia), the endemic Philippine tree mouse from Luzon Island.
	Soricomys leonardcoi	Rickart, E.A., Balete, D.S., Alviola, P.A., Veluz, M.J. & Heaney, L.R. (2016). The mammals of Mt. Amuyao: a richly endemic fauna in the Central Cordillera of northern Luzon Island, Philippines. *Mammalia*, 80, 579-592.
	Soricomys montanus	Rickart, E.A., Balete, D.S., Alviola, P.A., Veluz, M.J. & Heaney, L.R. (2016). The mammals of Mt. Amuyao: a richly endemic fauna in the Central Cordillera of northern Luzon Island, Philippines. *Mammalia*, 80, 579-592.

Table A3: Results of two-sided t-tests performed to determine whether turnover patterns differed from random sampling of the metacommunity (null model 1) and of the regional species pool (null model 2) for each metacommunity.

	Null model 1 (Metacommunity)								
	Taxonomic			Functional			Phylogenetic		
	μ	*t*	*p*	μ	*t*	*p*	μ	*t*	*p*
Adriatic	0.03	0.31	0.75	0.05	0.56	0.58	-0.18	**-2.38**	**0.019**
Alexander	0.03	1.04	0.30	-0.14	-6.77	**< 0.001**	-0.33	**-13.81**	**< 0.001**
California	-0.17	-1.35	0.18	0.32	2.78	**0.007**	-0.81	**-19.44**	**< 0.001**
Indonesia	0.02	0.41	0.68	0.21	3.98	**< 0.001**	-0.16	**-3.15**	**0.002**
Japan	0.00	-0.01	0.99	-0.03	-0.24	0.809	-0.12	-0.52	0.61
Maluku	0.06	0.32	0.75	-0.67	-5.57	**< 0.001**	0.60	**2.94**	**0.006**
Mediterranean	0.09	1.54	0.12	0.22	3.34	**0.001**	-0.23	**-4.36**	**< 0.001**
Melanesia	0.01	0.09	0.93	-0.18	-2.67	**0.008**	0.30	**2.13**	**0.03**
Philippines	0.06	0.81	0.42	-0.17	-4.10	**< 0.001**	0.10	1.29	0.20
	Null model 2 (Regional species pool)								
	Taxonomic			Functional			Phylogenetic		
	μ	*t*	*p*	μ	*t*	*p*	μ	*t*	*p*
Adriatic	-1.59	**-20.06**	**< 0.001**	0.34	**2.50**	**0.014**	0.01	0.11	0.91
Alexander	-1.86	**-50.30**	**< 0.001**	-0.70	**-49.75**	**< 0.001**	-0.14	-2.76	**0.006**
California	-0.87	**-5.16**	**< 0.001**	-0.01	-0.09	0.93	-0.97	**-17.74**	**< 0.001**
Indonesia	-1.85	**-17.36**	**< 0.001**	0.20	**3.84**	**< 0.001**	0.01	0.11	0.91
Japan	-1.69	**-6.32**	**< 0.001**	-0.29	**-2.72**	**0.01**	0.45	0.73	0.47
Maluku	-0.15	-0.43	0.67	-0.77	**-6.18**	**< 0.001**	1.22	**2.88**	**0.007**
Mediterranean	-1.48	**-23.67**	**< 0.001**	0.08	1.36	0.18	-0.05	-0.49	0.62
Melanesia	-0.75	**-5.39**	**< 0.001**	-0.08	-1.04	0.30	0.35	**2.21**	**0.028**
Philippines	-4.30	**-28.61**	**< 0.001**	-0.22	**-3.94**	**< 0.001**	0.21	**2.64**	**0.009**

μ = mean SESβSim within the metacommunity. Positive values indicate that communities are more dissimilar than expected from random sampling (i.e. higher turnover). Negative values indicate that communities are more similar than expected from random sampling (i.e. lower turnover); *t* = t-statistic; *p*: p-value for the test. Significant t-tests are bolded (i.e. p-value < 0.05).

Table A4: Explanatory environmental and spatial variables included in db-RDA models to explain taxonomic, functional, and phylogenetic turnover for each metacommunity after testing for collinearity and forward-selecting spatial variables.

	Environmental variables						Spatial variables
Taxonomic	Area	Elev	Temp	Prec	varT	varP	MEM
Alexander Archipelago		x	x	x	x	x	**1, 2, 3, 5, 6, 7**
Adriatic Sea	x			x	x	x	1, 2, 3
Gulf of California	x	x	x	x			1, 2, 3
Indonesia	x		x	x	x	x	1, 2, 3, 4, 5, 6, 7, 8
Japan		x			x	x	1, 2
Maluku Islands			x	x	x	x	1, 2, 3
Mediterranean		x	x	x	x		**1**
Melanesia		x	x	x	x	x	**1, 2, 3**
Philippines		x	x	x	x	x	1, 2, 3, 4, 5, 6, 7, 8, 9
Functional	Area	Elev	Temp	Prec	varT	varP	MEM
Alexander Archipelago		x	x	x	x	x	**1, 2, 3**
Adriatic Sea	x			x	x	x	1,2 3
Gulf of California	x	x	x	x			1, 2, 3
Indonesia	x		x	x	x	x	1, 2, 3, 4, 5, 6, 7, 8
Japan		x			x	x	1, 2
Maluku Islands			x	x	x	x	1, 2, 3
Mediterranean		x	x	x	x		1, 2, 3
Melanesia		x		x	x	x	1, 2, 3, 4, 5
Philippines		x	x	x	x	x	1, 2, 3, 4, 5, 6, 7, 8, 9
Phylogenetic	Area	Elev	Temp	Prec	varT	varP	MEM
Alexander Archipelago		x	x	x	x	x	**3**
Adriatic Sea	x			x	x	x	1,2 3
Gulf of California	x	x	x	x			1, 2, 3
Indonesia	x		x	x	x	x	1, 2, 3, 4, 5, 6, 7, 8
Japan		x			x	x	1, 2
Maluku Islands	x			x	x	x	1, 2, 3
Mediterranean		x	x	x	x		1, 2, 3
Melanesia		x		x	x	x	1, 2, 3, 4, 5
Philippines		x	x	x	x	x	1, 2, 3, 4, 5, 6, 7, 8, 9

x = variable included in db-RDA model. Environmental variables: Area = log-transformed island area; Elev = log-transformed maximum elevation; Temp = annual mean temperature; Prec = annual precipitation; varT = temperature seasonality; varP = precipitation seasonality. Spatial variables: MEM = numbered dbMEM eigenvectors. Bold indicates forward selection.

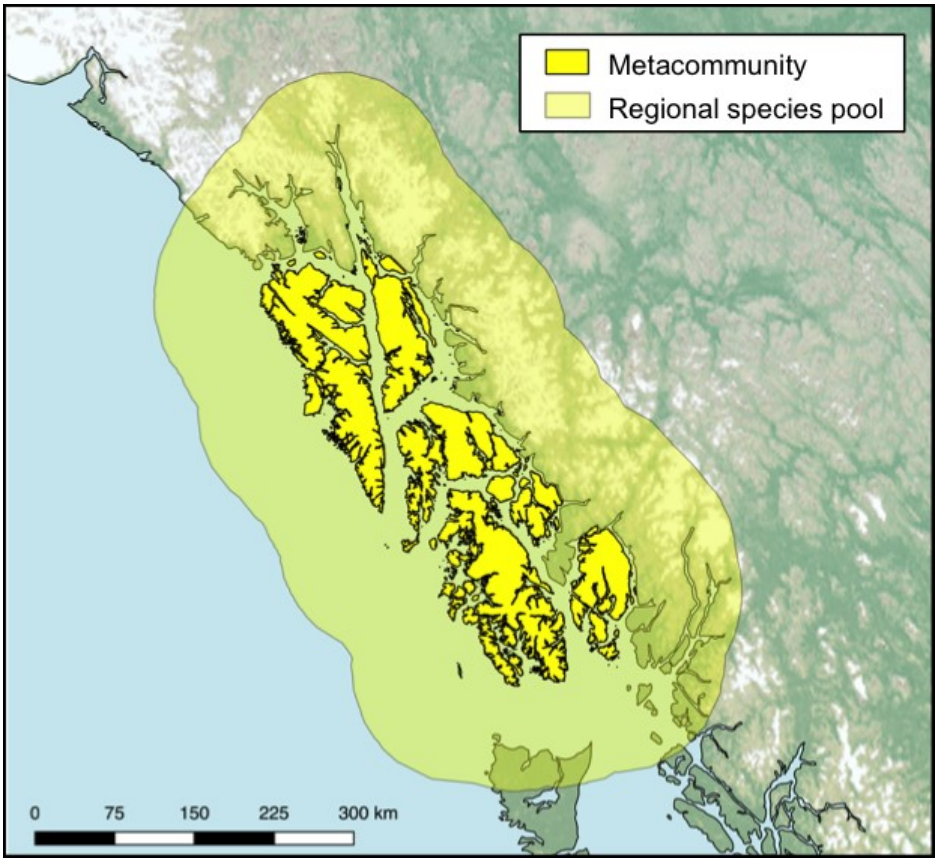

Figure A1: Map of the regional pool defined for the Alexander Archipelago metacommunity along the Alaskan coast, which includes any terrestrial non-volant mammal species whose geographic distribution touches or overlaps within the regional species pool area (in pale yellow).

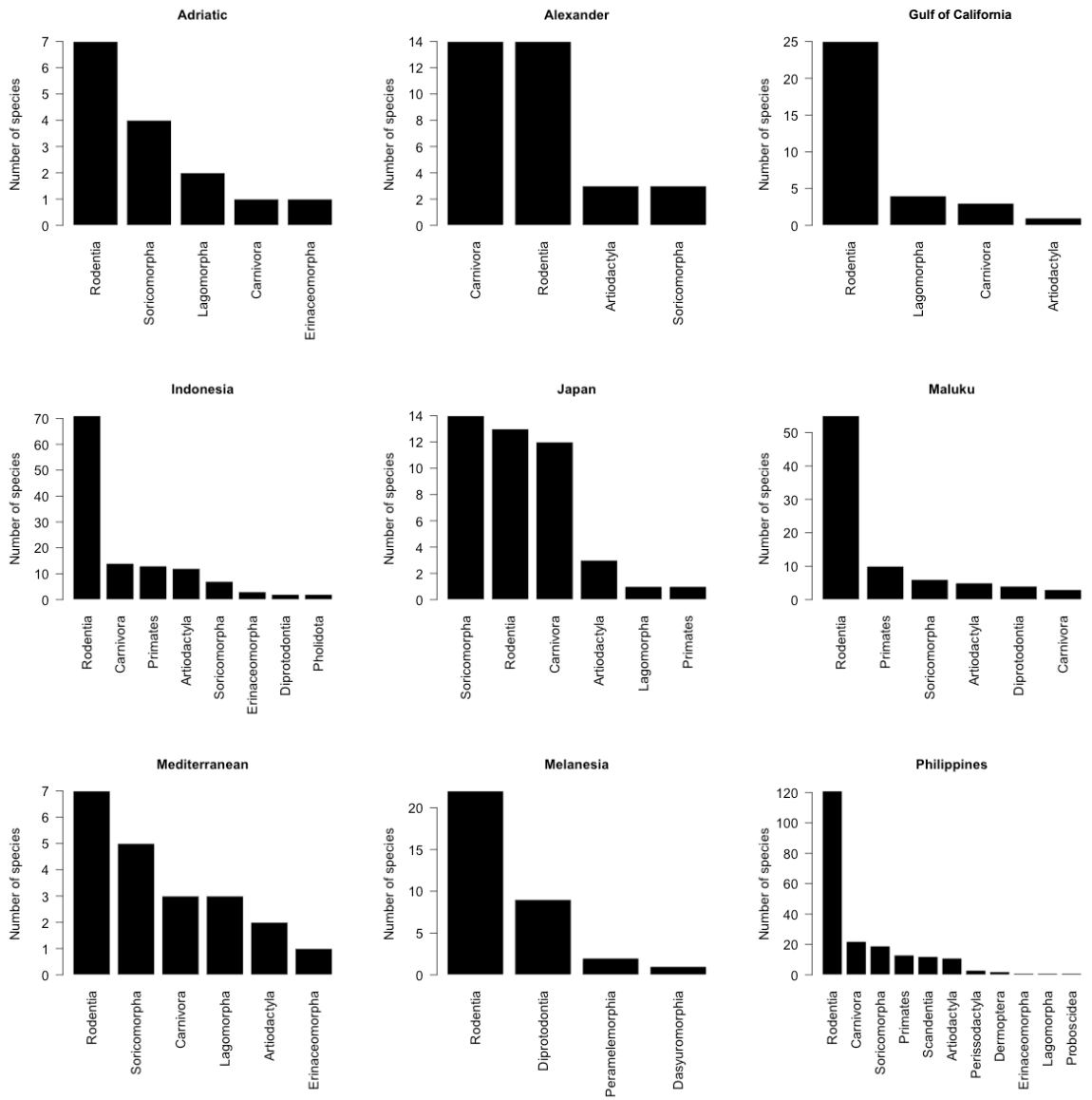

Figure A2: Number of species in all represented mammal orders within each of the 9 island metacommunities.

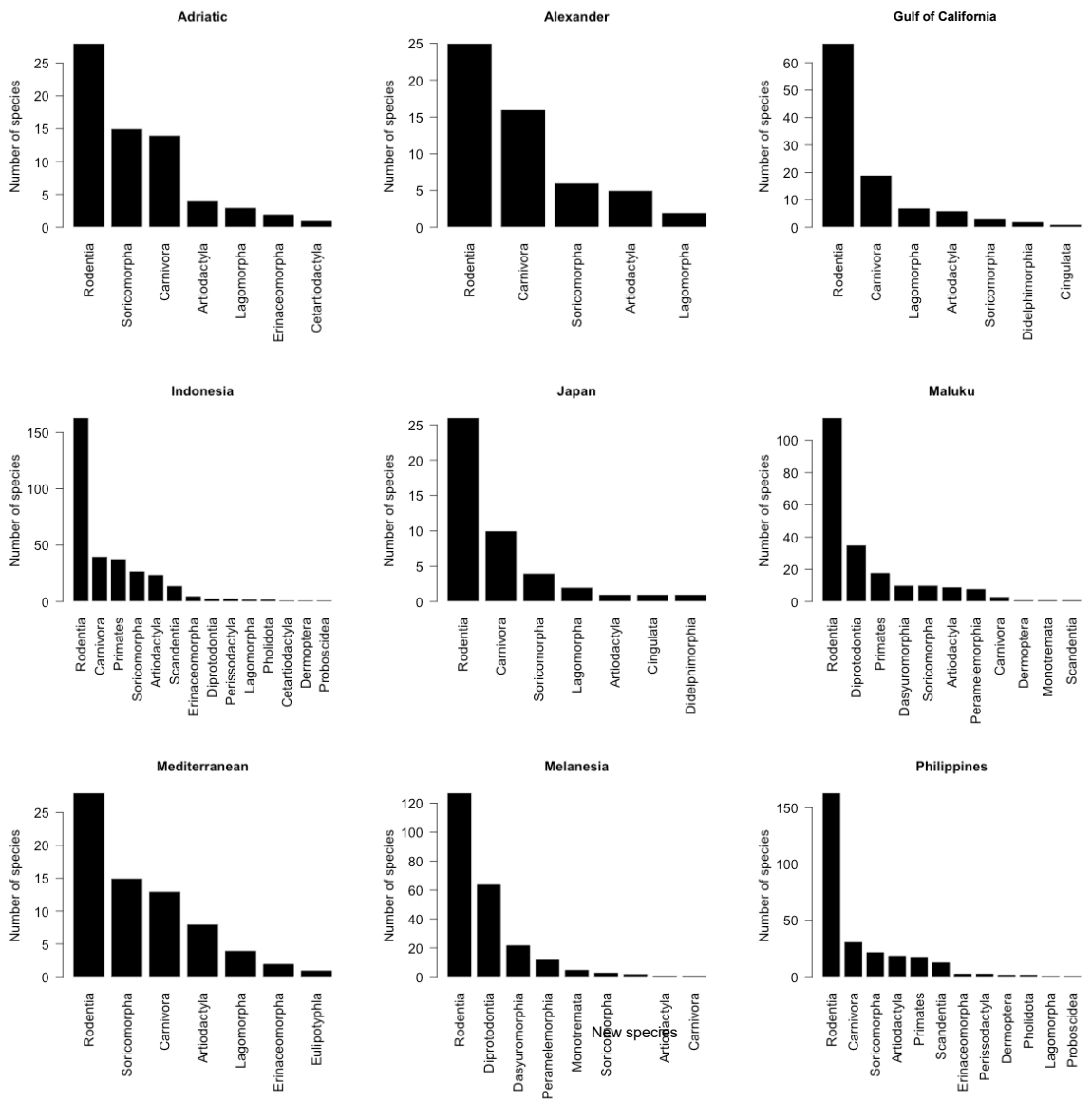

Figure A3: Number of species in all represented mammal orders included within each of the regional species pools, defined for each of the 9 island metacommunities.

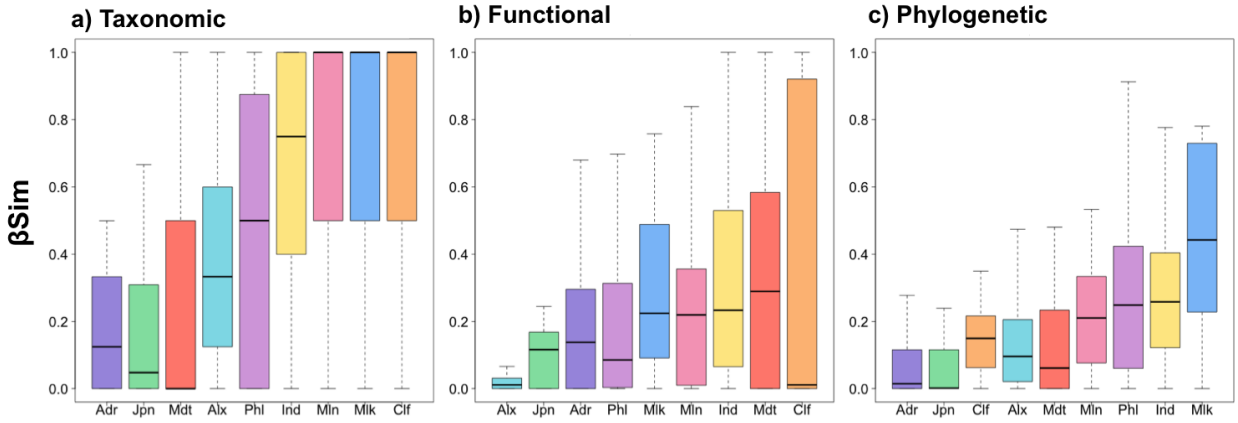

Figure A4: Observed β-diversity patterns within the metacommunities. (a) Observed taxonomic Simpson dissimilarities (TβSim). (b) Observed functional Simpson dissimilarities (FβSim). (c) Observed phylogenetic Simpson dissimilarities (PβSim). The boxplots are ordered by mean. Colours each designate a metacommunity (Fig. 1). The metacommunities are abbreviated as: Adr = Adriatic Sea, Alx = Alexander Archipelago, Clf = Gulf of California, Jpn = Japan, Ind = Indonesia, Mdt = Mediterranean, Mlk = Maluku, Mln = Melanesia, Phl = Philippines.

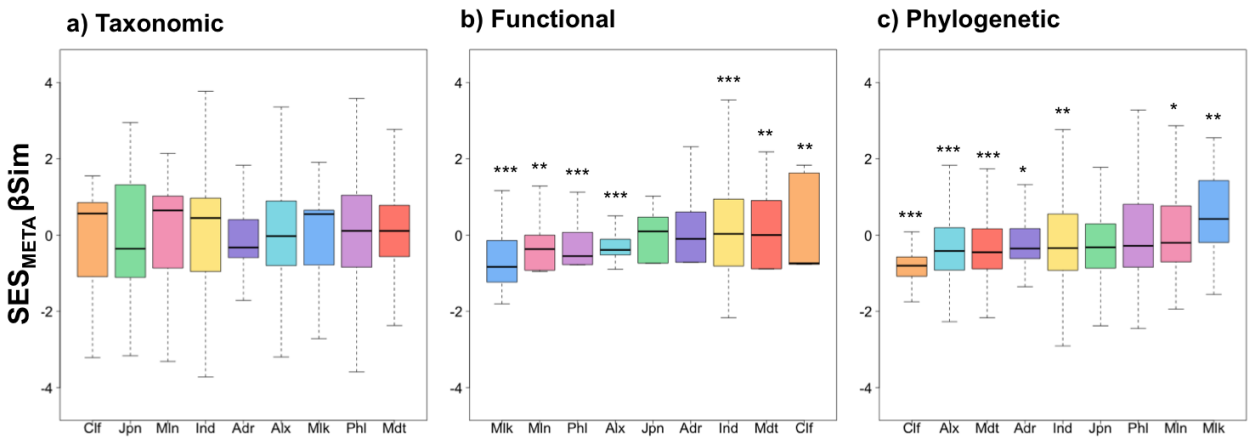

Figure A5: Standardized effect size of β-diversity patterns within the metacommunities under null model 1 for: (a) taxonomic Simpson dissimilarities (SES_{META}βSim), (b) functional Simpson dissimilarities (SES_{META}FβSim), and (c) phylogenetic Simpson dissimilarities (SES_{META}PβSim). The boxplots are ordered by mean. Colours each designate a metacommunity (Fig. 1). Metacommunities are abbreviated as: Adr = Adriatic Sea, Alx = Alexander Archipelago, Clf = Gulf of California, Jpn = Japan, Ind = Indonesia, Mdt = Mediterranean, Mlk = Maluku, Mln = Melanesia, Phl = Philippines. Asterisks indicate whether mean SES_{META}βSim is significantly different from 0: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

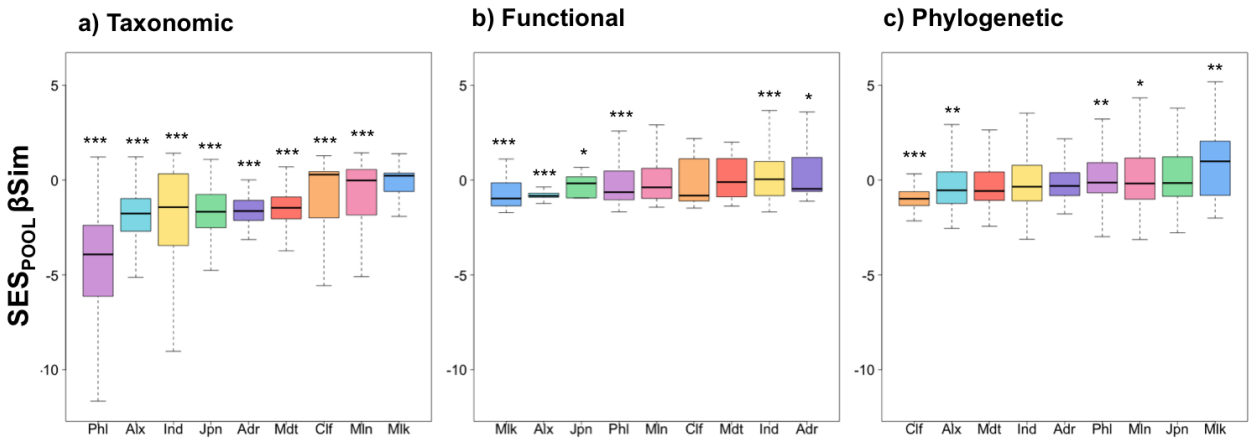

Figure A6: Standardized effect size of β-diversity patterns within the metacommunities under null model 2 for: (a) taxonomic Simpson dissimilarities (SES_{POOL} TβSim), (b) functional Simpson dissimilarities (SES_{POOL}FβSim), and (c) phylogenetic Simpson dissimilarities (SES_{POOL}PβSim). The boxplots are ordered by mean. Colours each designate a metacommunity (see Fig. 1). The metacommunities are abbreviated as: Adr = Adriatic Sea, Alx = Alexander Archipelago, Clf = Gulf of California, Jpn = Japan, Ind = Indonesia, Mdt = Mediterranean, Mlk = Maluku, Mln = Melanesia, Phl = Philippines. Asterisks indicate whether mean SES_{META}βSim is significantly different from 0: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.